Understanding current and potential distribution of Australian acacia species in southern Africa

by

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Declaration

I declare that this dissertation is my own work. It has been submitted for a Master of Science degree in Zoology at the University of Pretoria. It has not been submitted for any degree or examination at any other University. Chapter two of this dissertation has been published in *Neobiota* journal. As a result, content overlap may occur.

Signature **Date: June 2014**

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Understanding current and potential distribution of Australian *Acacia* species in southern Africa

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Abstract

This dissertation presents research on the value of using different sources of data to explore the factors determining invasiveness of introduced species. The research draws upon the availability of data on the historical trial plantings of alien species and other sources. The focus of the study is on Australian *Acacia* species as a taxon introduced into southern Africa (Lesotho, South Africa and Swaziland). The first component of the study focused on understanding the factors determining introduction outcome of species in historical trial plantings and invasion success of Australian *Acacia* species using Species Distribution Models (SDMs) and classification tree techniques. SDMs were calibrated using the native range occurrence records (Australia) and were validated using results of 150 years of South African government forestry trial planting records and invaded range data from the Southern African Plant Invaders Atlas. To understand factors associated with survival ('trial success') or failure to survive ('trial failure') of species in historical trial plantings, classification and regression tree analysis was used. The results indicate climate as one of the factors that explains introduction and/or invasion success of Australian *Acacia* species in southern Africa. However, the results also indicate that for 'trial failures' there are factors other than climate that could have influenced the trial outcome. This study emphasizes the need to integrate data

on whether the species has been recorded to be invasive elsewhere with climate matching for invasion risk assessment.

The second component of the study focused on understanding the distribution patterns of Australian *Acacia* species that are not known as invasive in southern Africa. The specific aims were to determine which species still exist at previously recorded sites and determine the current invasion status. This was done by collating data from different sources that list species introduced into southern Africa and then conducting revisits. For the purpose of this study, revisits means conducting field surveys based on recorded occurrences of introduced species. The known occurrence data for species on the list were obtained from different data sources and various invasion biology experts. As it was not practical to do revisits for all species on the list, three ornamental species (*Acacia floribunda*, *A. pendula* and *A. retinodes*) were selected as part of the pilot study for the conducted revisits in this study. *Acacia retinodes* trees were not found during the revisits. The results provided data that could be used to characterize species based on the Blackburn *et al*., (2011) scheme. However, it is not clear whether observed *Acacia pendula* or *A. floribunda* trees will spread away from the sites hence the need to continuously monitor sites for spread. The methods used in this research establish a protocol for future work on conducting revisits at known localities of introduced species to determine their population dynamics and thereby characterize the species according to the scheme for management purposes.

Keywords: Species distribution models, Southern African Plant Invaders Atlas, Forestry, Classification tree, expert knowledge, field visits, alien tree.

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1 General Introduction

Many tree species have been planted beyond their native ranges around the world for forestry and ornamental purposes. Some alien tree species that are of commercial importance cause major problems as invaders (Richardson, 1998; Pyšek *et al.*, 2009; Essl *et al.*, 2010; Nuñez & Medley, 2011). Commercial forestry is one of the known pathways that make a large contribution to species introduction (Essl *et al.*, 2010). Historically, species introduced for forestry were selected solely on the basis of their ability to serve the purpose of the introductions (e.g. timber production) with little concern of the negative effects like invasiveness (Essl *et al.*, 2010). Invasiveness is the extent to which an introduced species is able to overcome various biotic and abiotic barriers (Fig. 1.1), establish, proliferate, and disperse in a new environment (Wilson *et al.*, 2007; Blackburn *et al.*, 2011).

Biological invasions involve complex processes that include a series of events that an introduced species undergoes along the introduction-naturalization-invasion continuum (Fig. 1.1; Blackburn *et al.*, 2011; Hulme, 2012). The complexity of invasions depends on case-specific characteristics of each introduction and a variety of ecological phenomena including behavioural changes and potential lag times between establishment and invasion stages (Carlton, 1996; Sakai *et al.*, 2001; Wilson *et al.*, 2007; Hayes & Barry, 2008). Determinants of establishment that lead to invasions differ at each stage of the continuum, with introduction effort being generally important initially for tree species (Essl *et al.*, 2010).

Southern Africa is ranked among the five most invaded regions of the world (Richardson & Rejmánek, 2011; Rejmánek & Richardson, 2013). Globally, a total of 434 species of the 751 woody invaders are trees within 90 families (Rejmánek & Richardson, 2013). Richardson & Rejmánek (2011) indicated in their global review that most predominant invasive species are of the families Fabaceae and Pinaceae. Of the 23 *Acacia* species in the subgenus Phyllodineae that are known to be invasive globally, *Acacia mearnsii* has been reported as the most widespread species. *Pinus* and *Acacia* species are reported to be outstanding invaders with a wide range of adaptations that equip them to become invasive (Richardson, 1998) and feature most predominantly on worst invaders lists and the reviews of invasions globally.

The invasiveness of *Acacia* and *Pinus*, like many other taxa is correlated with the extent and duration of planting, emphasizing the importance of propagule pressure in explaining invasions (Richardson, 1998; Lockwood *et al.*, 2005; 2009). For example, Lockwood *et al.* (2005) indicated that the more individuals that are introduced into the new range, the greater the likelihood for those individuals to form populations that will survive, become self-sustaining and invade that range. Wilson *et al.* (2007) indicated that the longer the species has been introduced into the new range, the greater the likelihood for such species to invade that range ('duration of planting'). However, apart from the current extent of planting of pines and wattles, it is likely that many more species will be introduced as the demand for products derived from such species increases. To mitigate or reduce alien tree invasions, we need to distinguish between damaging and innocuous species for management and policy making (De Wit *et al.*, 2001).

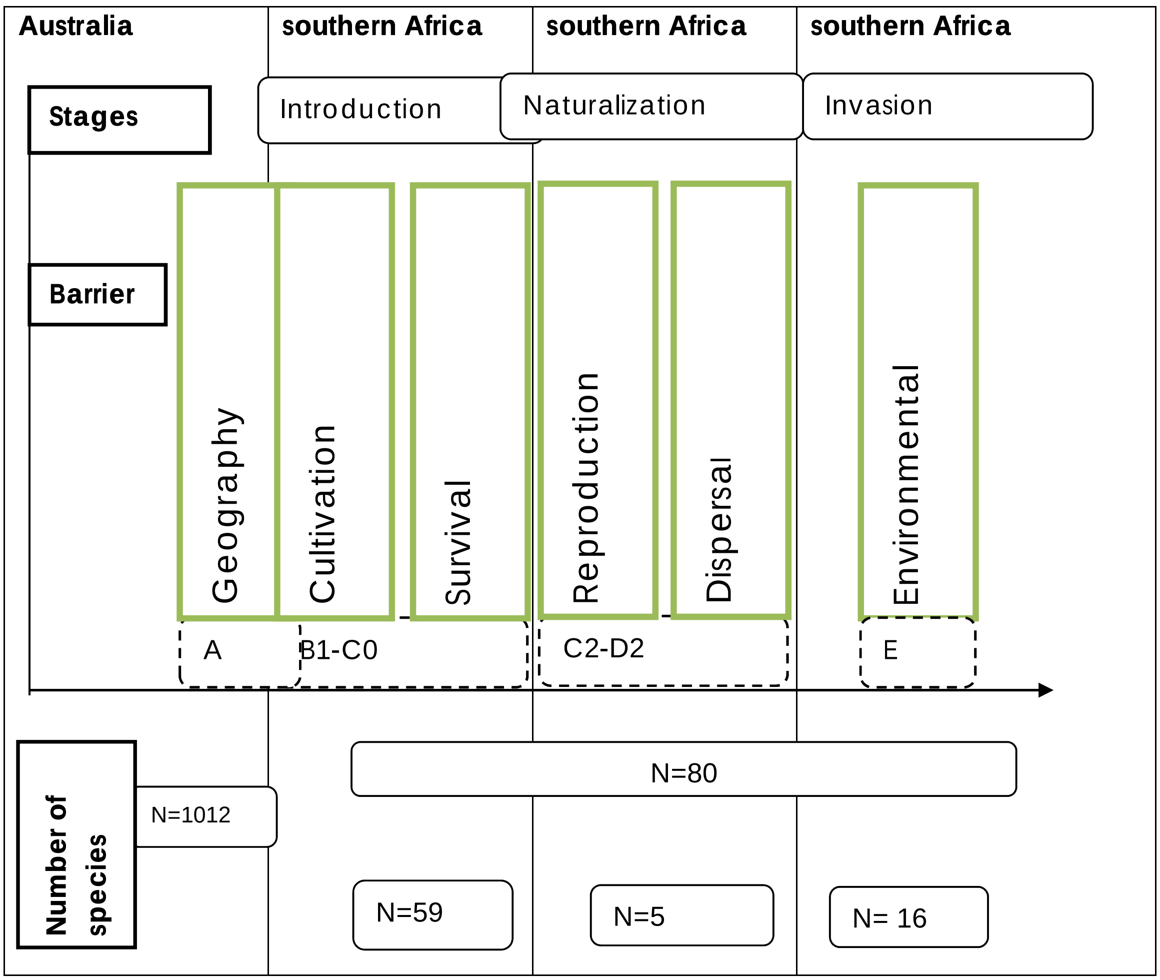


Figure 1.1: Schematic presentation of the progression of an invasion with relevant categories, stages and barriers as described by Blackburn *et al.*, (2011). The total number of Australian *Acacia* species in the native range (Australia) and the introduced range (southern Africa) as obtained from herbarium records and forestry trials and edited from Richardson *et al.*, (2011). The currently known invasive status in the introduced range is also indicated.

One research focus of invasion biology is to determine ways that can be used to prevent the introduction of new species or to detect and eradicate potentially high-risk species before they become major invaders (Scott & Panetta, 1993; Reichard & Hamilton, 1997; Pheloung *et al.*, 1999; Daehler *et al.*, 2004). This is relevant as South Africa has limited resources available for management of invasive alien species and management has been reactive in nature (i.e. to control species that are already widespread and abundant). For example, the Working for Water Programme is commended for their innovative approach for managing invasive alien species (Mgidi *et al.*, 2007) but the most of their work has to deal with species that are already invasive. Research has recently focused on pro-active management approaches with the main aim of developing tools that can be used to detect potential invaders prior to the introduction of target species into new range (i.e. pre- border risk assessment *sensu* Wilson *et al*., 2013) and after the target species has been introduced and on the introduction-naturalization-invasion continuum (i.e. post-border risk assessment *sensu* Wilson *et al*., 2013).

Pre-border risk assessments include the prediction of the potential behaviour of the alien target species prior to its introduction (Scott & Panetta, 1993; Reichard & Hamilton, 1997; Pheloung *et al.*, 1999; Daehler *et al.*, 2004). The screening procedures depend on species attributes and some ecological interactions (Rejmánek *et al.*, 2005). The schemes used to predict potential behaviour of species rely largely on the scoring or rating schemes or hierarchical decision trees. Hulme (2012) indicated that schemes used for predicting potential behaviour of introduced species are not better than simply considering prior invasion history and climatic match between native and introduced ranges for a target species.

Post-border risk assessment models focus on predicting the future behaviour of species that are already introduced into the region or country, and might be naturalized but not yet invasive (Richardson *et al.*, 2000; Blackburn *et al.*, 2011). Wilson *et al.* (2013) indicated that surveying sites of known occurrences of introduced but not yet invasive plant species as one method of detecting new invaders. This is of particular importance as population growth of introduced species may drive successful establishments leading to invasions (Zenni *et al.*, 2009; Kaplan *et al.*, 2012). In addition, climatic matching techniques and species traits have been used to predict the invasiveness of introduced alien tree species (Castro-Díez *et al.*, 2011; McGregor *et al.*, 2012a)..

Species distribution models

Species Distribution Models (SDMs) also known as bioclimatic models, ecological niche models and habitat models have been widely used in various studies that focused on understanding invasions (Thuiller *et al*., 2005; Broennimann & Guisan, 2008; McGregor *et al*., 2012a). An SDM is a mathematical description of the species distribution in environmental space that can be used to predict the distribution of species in geographic space (Peterson *et al*., 1999). The SDM applications in invasion biology allow for predictions to be extended beyond the geographic and environmental region from which the training samples were drawn (Araújo *et al*., 2005). The models combine species occurrence records and environmental variables to create a climatic envelope model (Peterson & Holt, 2003). The models combine species occurrence records in the native, introduced or both ranges with climatic variables to create a predictive model of species requirements for the predictors examined (Steiner *et al*., 2008). The climatic variables are chosen based on the ecology and biology of a target species. The resulting model can be projected to any geographic space to identify regions that are climatically suitable for target species. SDMs can therefore be used to identify areas that are suitable for species even before introduction to predict which areas are likely to be invaded (Guisan & Zimmermann, 2000).

Generally, in research the use of SDMs in invasion biology is improved by the use of native and introduced occurrence data. For example, SDMs calibrated using native range to extrapolate climatic ranges of target species have been validated using introduced range data for that species (Rouget *et al*., 2004; Nel *et al*., 2004; Thompson *et al*., 2011) and the relationship between model predictions and validation data is quantified using several measures inlcuding Kappa statistics, Area Under Curve and True Skill Statistics (Fielding & Bell, 1997; Allouche *et al*., 2006).

Ideally, introduced range occurrence datasets should contain information on species that were repeatedly introduced in different localities with a clear indication of introduction outcome (i.e. whether introduced species survived after introduction ‘success’ or whether the introduced species did not survive ‘failure’). It is important that the records on introduction outcome explicitly indicate which factors influenced the outcome (e.g. climate or biotic). However, these ideal datasets are not always available. An exception to this is the documentation of forestry trials that include information on trial success or failures in different parts of southern Africa (Poynton, 1979a, 1979b, 2009). The forestry trial dataset is the result of 150 years of trials that were performed by the governments of different southern African countries, but the study focused on trials that were performed in Lesotho, South

Africa and Swaziland. Data include geographic coordinates of stations where trials were performed for pines, eucalypts and other genera. Historical trial plantings publications provide useful data for studying species distributions.

Australian Acacia species

Australian *Acacia* species (commonly known as wattles) are a group of 1012 species in the genus *Acacia* subgenus *Phyllodineae* that are native to Australia (Miller *et al.*, 2011). Australian *Acacia* species have been introduced to different parts of the world for various reasons (Breton *et al.*, 2008; Kull *et al.*, 2011). Currently, 23 Australian *Acacia* species are considered invasive in at least one part of the world (Richardson *et al.*, 2011). Self-sown stands of many species dominate different landscapes in many parts of the world with different degrees of *invasiveness* (Castro-Díez *et al.*, 2011; Richardson *et al.*, 2011). *Acacia mearnsii* is listed as the most widespread Australian *Acacia* species in the world as it is invasive in twelve countries (Richardson & Rejmánek, 2011). Other *Acacia* species are only moderately weedy while others are not yet known to invade landscapes, although they might have only been recently introduced (Gaertner *et al.*, 2009; Castro-Díez *et al.*, 2011; Richardson & Rejmánek, 2011).

Australian *Acacia* species have severe impacts in invaded ecosystems and similar impacts are likely to emerge in other areas where species have been introduced (De Wit *et al.*, 2001; Le Maitre *et al.*, 2002; Le Maitre *et al.*, 2011). The impacts caused by Australian *Acacia* species include a reduction of surface stream flow (due to increased rainfall interception and increased transpiration), displacement of indigenous plant communities, and alteration of soil properties (specifically increased levels of nitrogen in the soil which can make habitats unsuitable for indigenous plants), the latter two leading to reductions in biodiversity (De Wit *et al.*, 2001; Coetzee *et al.*, 2007; Gaertner *et al.*, 2009; Le Maitre *et al.*, 2011).

Australian *Acacia* species are reported as an important group in terms of forestry, ornamental and landscape architecture purposes (Kull & Rangan, 2008; Kull *et al.*, 2011; Kull & Tassin, 2012). Worldwide regional movements of cool-climate, tropical and arid zone *Acacia* species (*Acacia mearnsii*, *A. dealbata*, *A. melanoxylon*, *A. mangium*, *A. crassicarpa*, *A. auriculiformis*, *A. colei* and *A. cowleana*) were mainly for forestry and ornamental purposes (Kull & Rangan, 2008). This increased the need for methods that can ensure sustainable use (commercial, aesthetic and environmental protection) as the group is of commercial value but also reported to be among the group of major invaders of natural ecosystems. Therefore, there is a need for risk assessment schemes that will separate potential invasive species from non-invasive species to reach sustainable use (Wilson *et al*., 2007).

Australian Acacia species in southern Africa

Early introductions of Australian *Acacia* species in southern Africa included several species that could provide timber and stabilise sand (Le Maitre *et al.*, 2011). In the 20th century government-funded schemes hired unemployed people to afforest large areas as forestry crops (Shaughnessy, 1980; Poynton, 2009). Although Australian *Acacia* species are important for the forestry industry in the region, some species are reported to be on the list of worst invaders (De Wit *et al.*, 2001; Le Maitre *et al.*, 2002; Gaertner *et al.*, 2009; Wilson *et al.*, 2011).

Currently, 80 Australian *Acacia* species that have been introduced into southern Africa, as determined from herbarium records and forestry trials (Fig. 1.1; Richardson *et al.*, 2011) of which sixteen are listed as invasive with an additional five species listed naturalized species (Henderson, 2007; van Wilgen *et al.*, 2011; Wilson *et al.*, 2011). Southern Africa has many Australian *Acacia* species that are currently at low densities that might become widespread as their populations grow and spread away from planting sites (Poynton, 2009). This suggests that there is a possibility of more invasions from introduced species that are not yet invasive.

The increasing invasions caused by Australian *Acacia* species have become a matter of concern because of the impacts they cause. In 1996, it was estimated that the condensed area of ca. 643 000 ha in southern Africa to be covered by Australian *Acacia* species (*sensu* Le Maitre *et al.*, 2000; van Wilgen *et al.*, 2011). Le Maitre *et al.* (2000) explained a condensed area as the reduced size of invaded range to its equivalent had the canopy cover been 100%. Le Maitre *et al.* (2000) also provided an example to further describe the 'condensed area' as an area of 100 ha with 50% cover as equivalent mathematically to a condensed area of 50 ha with 100% cover. Kotzé *et al.*, (2010) indicated that this area has decreased by an estimated 14% to 554 000 ha. van Wilgen *et al.,* (2011) proposed that the role of biological control and substantial harvesting of firewood for *Acacia cyclops* and biological control on *A. saligna* can explain the decline of infested area.

Between the years 2000 and 2010, 135 000 ha of South Africa that was covered by invasive Australian *Acacia* species was cleared by the Working for Water programme (van Wilgen *et al.* 2011). This was done at a cost of about ZAR 880 million (Shackleton *et al.*, 2011). De Wit *et al.* (2001) estimated the cost of clearing widespread and abundant invaders (*Acacia mearnsii*) total invaded area to be $1426 million (R6=1US$) in 1998. There have also been several recent estimates for the cost of eradicating small and localized populations of *Acacia implexa*, *A. paradoxa* and *A. stricta.* Kaplan *et al.* (2012) estimated the cost of clearing 600 ha of South Africa covered by *A. implexa* to be ZAR 683 300. Moore *et al.* (2011) predicted that it will cost ZAR 8 million to clear *Acacia paradoxa* populations in South Africa.

Why are Australian Acacia species successful invaders?

Recently, several studies were conducted by invasion biologists to evaluate invasiveness of Australian *Acacia* species around the world (Gallagher *et al*., 2011; Richardson *et al*., 2011; Wilson *et al*., 2011). The main findings indicated that this group will continually invade semi-natural and natural ecosystems worldwide (Wilson *et al*., 2011). This emphasizes the need for more detailed research focussing on Australian *Acacia* species especially dealing with predicting invasions. The studies should include pre-border risk assessment for species that are not yet introduced into different parts of the world and other naturalized or already invasive species in their introduced ranges.

Morris *et al.* (2011) indicated that Australian *Acacia species* have ecophysiological traits that enable them to compete for resources and dominate *native* species. Australian *Acacia* species are well known for their ability to efficiently fix atmospheric nitrogen (Levine *et al.*, 2003). Australian *Acacia* species like other legumes form a symbiotic relationship with a nitrogen fixing bacteria that facilitate nitrogen fixation into essential organic molecules (Rodríguez-Echeverría *et al*., 2011). Rodríguez-Echeverría *et al.* (2012) indicated that some of the nitrogen fixing bacteria called bradyrhizobia have detrimental effects on native shrubs while promoting growth of co-occurring Australian *Acacia* species. Decomposition of sclerophyllous phyllodes and leaves from Australian *Acacia* species result in soil nutrient alteration (Morris *et al*., 2011). The legacy of soil rich in nitrogen hinders the competitive abilities of the native species and enhances invasions (Morris *et al*., 2011).

Gibson *et al.* (2011) indicated that there are sets of reproductive traits that enable Australian *Acacia* species to reproduce effectively in their introduced ranges. Such traits include early maturation that leads to faster accumulation of seeds leading to large seed banks (Richardson & Kluge, 2008) and resprouting abilities. Hui *et al.* (2011) also indicated that invasiveness in Australian *Acacia* species is linked to high population increase rate. The ability of Australian *Acacia* species to produce seeds in massive numbers and accumulate the seeds in seed banks contribute to their invasiveness, although these attributes alone do not guarantee invasiveness (Gibson *et al.*, 2011; Morris *et al.*, 2011).

Australian *Acacia* species are widely used for various purposes (Kull *et al.*, 2011; Kull & Tassin, 2012) and their invasiveness is linked to their likelihood of being disseminated to and within new regions, thus increasing the risk of invasion. Propagule pressure and residence time have been indicated as drivers of different patterns observed for the distribution of Australian *Acacia* species in southern Africa (van Wilgen *et al.*, 2011; Wilson *et al.*, 2011). The extent and propagation of Australian *Acacia* species in southern Africa has been linked to invasiveness over time. As such, there is a considerable chance that many Australian *Acacia* species will expand their ranges into climatically suitable but as yet unoccupied areas.

Biogeographic factors like large native range size and climatic suitability in the introduced range increase the likelihood that an introduced species will be invasive (Gallagher *et al.*, 2011; Hui *et al.*, 2011). Rouget *et al.* (2004) indicated that even widespread Australian *Acacia* species like *Acacia mearnsii* are likely to expand their current ranges as there are still unoccupied areas that are suitable. Invasive Australian *Acacia* species differ substantially in their extent of invasion, for example eleven species are widespread while other species are naturalized or occur only at one site. There are also several introduced species that have not yet been reported as naturalized or invasive (Poynton, 2009). This indicates the possibility of an invasion debt (*sensu* Essl *et al.*, 2011a) that needs to be reduced by management strategies that focus on all stages of the introduction-naturalization-invasion continuum (Blackburn *et al.*, 2011; Wilson *et al.*, 2011). Essl *et al.* (2011b) indicated that biological invasions are not caused by species that are recently arrived in the new range and proposed ‘invasion debt’ as a phenomenon that explain current patterns of alien-species richness as better reflecting historical rather contemporary human activities.

1.1 Background and Context

Predicting which introduced Australian *Acacia* species will become invasive requires, among other things, data on their occurrences in either native or introduced ranges. Records that list introductions are essential tools in risk assessment, although they are not easily accessible (McGeoch *et al.*, 2012). In South Africa, government forestry trial plantings were conducted throughout the region to determine which areas are suitable for a range of candidate Australian *Acacia* species that were being considered for cultivation. The performance of each trial per species was recorded and monitored (Poynton, 2009). These records are useful when explaining successes (i.e trials where planted species survived) or failures (trials where planted species did not survive) of species in trials as it clearly provides an account of each trial and the reasons why species failed in trials. Trial successes are used in this study as presences and trial failures as absences to indicate occurrences of species. In addition to this publication on forestry trial plantings (Poynton, 2009), a frequently used database of invasive and naturalized species: Southern African Plant Invaders Atlas was used (Henderson, 1998), herbarium specimens, Pretoria herbarium Computerized Information System (PRECIS) and invasion biology expert knowledge data were used as records of known occurrences of Australian *Acacia* species in southern Africa in this study. The first component of the study focused on using forestry trial plantings and SAPIA data together with climate-based SDMs to understand Australian *Acacia* invasions. The second component focused on species that are not known as invasive in southern Africa, with an aim of understanding the current invasion status based on conducted revisits and literature. Revisiting known records of introduced species is valuable for management of invasive alien species as it is important to know whether the recorded plant still exists, its current status and its ability to spread.

1.2 Aims and Objectives

The focus of the first component of this study draws upon the availability of native occurrence records of Australian *Acacia* species together with historical trial plantings and invaded range data in the introduced range (southern Africa). The aims of this component were to explore factors that determine the introduction and/or invasion success of this taxon in southern Africa. The approach was to determine how well climate-based models can predict 1) trial outcome of Australian *Acacia* species that were planted as historical trials, 2) invaded ranges; and 3) determine which of the introduced species that are not yet invasive have climatically suitable ranges in southern Africa; and lastly to determine other factors that can explain the variability of introduction outcome of species in historical trial plantings not captured by the SDMs.

The second component of the study focused on the use of known occurrences of Australian *Acacia* species that are not yet invasive to assess the current invasive status in southern Africa based on both literature and results obtained from revisiting trails. To do this, the maps were generated maps understand the occurrence patterns of such species and then the surveys were conducted at known sites of these species and ultimately the protocol that can be used to revisit recorded occurrences of introduced species was developed.

1.3 Overview of the Dissertation

This dissertation is divided into four chapters with the first chapter being the general introduction (this chapter) which introduces the topic, the second chapter explores the use of forestry trial and SAPIA data to validate SDM prediction in understanding tree invasions and the use of classification trees to understand forestry trial planting outcome; and the third chapter focuses on the use of available known occurrence data in preliminary surveys (‘revisits’) of Australian *Acacia* species that are not yet widespread in southern Africa to understand the invasion status and finally the fourth chapter provides a general discussion of the results that were obtained in the second and third chapters, emphasizing the implications for Australian *Acacia* species invasion management in southern Africa.

2 Forestry trial data can be used to evaluate climate-based species distribution models in predicting tree invasions

Abstract

Climate is frequently used to predict the outcome of species introductions based on the results from SDMs. However, despite the widespread use of SDMs for pre- and post-border risk assessments, data that can be used to validate predictions is often not available until after an invasion has occurred. Here we explore the potential for using historical forestry trials to assess the performance of climate-based SDMs. SDMs were parameterized based on the native range distribution of 36 Australian *Acacia* species, and predictions were compared against both the results of 150 years of South African government forestry trials, and current invasive distribution in southern Africa using true skill statistic, sensitivity and specificity. Classification tree analysis was used to evaluate why some Australian *Acacia* species trials failed (species did not survive) whilst others were successful (species survived). Predicted climatic suitability was significantly related to the invaded range (sensitivity = 0.87) and success in forestry trials (sensitivity = 0.80), but forestry trial failures were under-predicted (specificity =0.35). Notably, for forestry trials, the success in trials was greater for species invasive elsewhere in the world. SDM predictions also indicate a considerable invasion potential of eight species that are currently naturalized but not yet widespread. Forestry trial data clearly provides a useful additional source of data to validate and refine SDMs in the context of risk assessment. Our study identified the climatic factors required for successful invasion of *Acacia* species, and accentuates the importance of integration of status elsewhere for risk assessment.

Keywords Model evaluation, Australian *Acacia* species, classification tree, forestry, alien trees, invasions, Southern African Plant Invaders Atlas

2.1 Introduction

Predicting which species will escape from forestry plantations and become invasive remains a challenge in invasion biology (Daehler *et al.*, 2004). Such prediction is an essential requirement for proactive management (Ficetola *et al.*, 2007). Propagule pressure, residence time, species traits, environmental factors, interactions of introduced species with the native species and historical factors have all been indicated as drivers of invasion success (Křivánek *et al.*, 2006; Thuiller *et al.*, 2006; Wilson *et al.*, 2007; Lockwood *et al.*, 2009; Pyšek *et al.*, 2009; Castro-Díez *et al.*, 2011), with invasion from siviculture as no exception (Castro-Díez *et al.*, 2011; Gallagher *et al.*, 2011). However, climate plays a fundamental role in determining species distributions (Gaston, 2003), and the predictive success of invasive risk assessments is still largely a function of invasiveness elsewhere and climate suitability (Hulme, 2012).

While alien (non-native, introduced) trees and shrubs have been introduced in different parts of the world to fulfil a wide range of human needs (Richardson & Rejmánek 2011), historically forestry has been one of the most important pathways (Pyšek *et al.*, 2009; Pyšek *et al.*, 2011). Introduced forestry species contribute to the economies of many countries, but can also cause major problems as invaders of natural and semi-natural ecosystems (Essl *et al.*, 2010; Essl *et al.*, 2011b; Richardson & Rejmánek, 2011). Research indicates that species that were introduced for forestry were selected solely because of the ability to serve the purpose of introduction and negative impacts like invasiveness were not considered (Essl *et al*., 2010).

Species Distribution Models have been widely used to understand climatic factors associated with invasions (Peterson, 2003; Pauchard *et al.*, 2004; Zhu *et al.*, 2007; Elith & Leathwick, 2009). SDMs have considerable potential in risk assessment but they are seldom tested in predicting successful tree establishments but see (Nuñez &Medley 2011). Observed distribution data from the native range of a species is often used to model their climatic niche, and projected at global scale to locate the areas where the target species is likely to establish. The availability of data on native distribution records of Australian *Acacia* species, and new modelling techniques gives an opportunity to understand invasions (Richardson *et al.*, 2011).

The use of SDMs in management of invasive species can be considerably improved by independent datasets that can be used to validate SDM predictions (Fielding & Bell 1997; Allouche *et al*., 2006). This means that the relationship between model predictions and independent datasets of the target species can provide a measure of how useful the models are. Appropriate datasets should contain information on species that were repeatedly introduced in different localities with a clear indication of introduction outcome (i.e. whether the species survived or not after introduction). It is important that the records on introduction outcome explicitly indicate which factors influenced the outcome (e.g. climate or biotic).

The ideal datasets are rarely available. Therefore invaded range data have been used to validate SDMs predictions (Wilson *et al*., 2007; Nuñez & Medley, 2011; McGregor *et al.*, 2012a). However, such analyses are limited to established widespread invasive species, ignoring any failed introductions. In southern Africa, experiments or trials on plantings of different tree species have been well documented and reviewed by Poynton (1979a, 1979b; 2009). The data from these trials provide historical information that includes the trial outcome, making it possible to explore factors influencing the success of introductions across different areas.

In southern Africa, forestry trials for Australian *Acacia* species were conducted at 67 sites from the 1820s to the 1960s for 36 species (Poynton, 2009). These data include records on introduction date for some species and number of sites where a target species was planted. This type of data can be used in studies that seek to quantify the importance of introduction history in explaining invasions (Wilson *et al*., 2007). The forestry trials dataset covers ten countries (Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia, and Zimbabwe), i.e. most of southern Africa. In the current study, only records in Lesotho, South Africa and Swaziland were used, as the trial data were well-represented for these countries.

Australian *Acacia* species are a good model group to understand plant invasions because *Acacia* is a speciose genus that contains many introduced and invasive species (Richardson *et al*., 2011). They are also a good group for exploring SDMs because native ranges in Australia and introduced ranges in southern Africa are well known and documented, e.g. the earliest introduction records of Australian *Acacia* species to southern Africa date back to 1800s (van Wilgen *et al*., 2011). Around 80 Australian *Acacia* species have been introduced in southern Africa, 36 of which were included in forestry trials (Richardson *et al*., 2011; Poynton 2009,Table 1.1). Currently, sixteen *Acacia* species are confirmed as invasive and three species are reported to be naturalized, but it is not clear which species is likely to invade the region and whether invasive species ranges will expand in the future (Richardson *et al*., 2011; Richardson & Rejmánek, 2011; van Wilgen *et al*., 2011; Wilson *et al*., 2011). This study was conducted in part to determine which species have large portions of the region that are climatically suitable, hence the probability of range expansion leading to invasions.

This component of the study draws upon the availability of native occurrence records (Australia) of Australian *Acacia* species together with data on historical trial plantings and occurrence records from introduced range (southern Africa) and aimed to determine climatic factors (i.e. rainfall and temperature-related) that determine the introduction and/or invasion success of this taxon in southern Africa. The approach was to determine how well climate-based models can predict 1) trial outcome of Australian *Acacia* species that were planted as historical trials, 2) invaded ranges 3) determine which of the introduced species that are not yet invasive have climatically suitable ranges in southern Africa; and lastly to determine other factors that can explain the variability of introduction outcome of species in historical trial plantings not captured by the SDMs.

Table 1.1: Australian *Acacia* species introduced into southern Africa, the number of trial sites (n) and number of sites occupied by species from historical trial planting, the number of sites invaded in Southern African Plant Invaders Atlas (SAPIA), the number of quarter degree grid cells occupied (QDGCs) in Lesotho, South Africa and Swaziland and status in southern Africa.

Species	Total number of sites for trials	Sites with successful trials	Sites invaded in southern Africa	QDGCs occupied in southern Africa	Invasive status in Southern Africa
A. acuminata	13	3	0	0	Introduced
A. adunca	1	0	2	2	Naturalized
A. adsurgens	2	2	0	0	Introduced
A. aneura	4	3	0	0	Introduced
A. aulacorpa	4	2	0	0	Introduced
A. auriculiformis	3	2	0	0	Introduced
A. baileyana	5	4	184	101	Invasive
A. binervata	1	1	0	0	Introduced
A. cowleana	2	1	0	0	Introduced
A. crassicarpa	2	1	0	0	Introduced
A. cultriformis	7	3	1	1	Naturalized
A. cyclops	2	2	1282	172	Invasive
A. dealbata	13	12	1667	299	Invasive
A. decurrens	5	2	341	124	Invasive
A. elata	9	3	99	48	Invasive
A. falciformis	4	2	0	0	Introduced
A. fimbriata	1	1	1	1	Naturalized
A. holosericea	4	1	1	0	Introduced
A. implexa	0	0	3	3	Invasive
A. leptocarpa	2	2	0	0	Introduced
A. ligulata	1	1	0	0	Introduced
A. longifolia	5	4	446	97	Invasive
A. mangium	3	1	0	0	Introduced
A. mearnsii	13	10	4313	462	Invasive
A. melanoxylon	28	20	678	167	Invasive
A. paradoxa	1	1	4	2	Invasive
A. pendula	6	3	0	0	Introduced
A. podalyriifolia	3	2	159	78	Invasive
A. prominens	2	2	0	0	Introduced
A. pycnantha	9	8	182	38	Invasive
A. retinodes	2	2	0	0	Introduced

A. rubida	1	1	0	0	Introduced
A. saligna	8	5	1302	164	Invasive
A. schinoides	1	1	0	0	Introduced
A. stricta	0	0	6	6	Invasive
A. viscidula	1	1	1	1	Naturalized
Total	**168**	**109**	**10672**	**1766**	

2.2 Methods

2.2.1 Study species and occurrence data

To evaluate the role of climatic factors associated with Australian *Acacia* species trial outcome (trial success or failure) and invasion success, SDMs were developed for 36 species using occurrence data from their native range and determined whether the models can predict introduction success in southern Africa (Table 1.1). Models were created using native distribution data obtained from the Australian Virtual Herbarium online database (http://avh.rbg.vic.gov.au, accessed 29th June 2010). Australian *Acacia* occurrence records in South Africa were represented by sites where the species were planted as trials. For the purpose of this study sites where species survived are called 'trial success' and where the species did not survive are 'trial failure'. The model predictions were validated using both South African government forestry trial plantings (Poynton, 2009) and invaded range data from Southern African Plant Invaders Atlas (Henderson, 2007; accessed January 2012).

Government forestry trials

Historical trial plantings data was compiled from the recent publication on tree plantings in southern Africa (Poynton, 2009). Poynton (2009) contains statements that provide data on how each species performed in each trial per station. The geographic locality of each station is given as Appendix A of this publication. All records that had unclear trial outcome descriptions and non-specific locality points were excluded. For example, this statement was given for one trial for *Acacia podalyriifolia*: "The pearl *Acacia* has been grown in South Africa for many years, particularly in the coastal regions, but only in recent years it has been widely planted in the Highveld".

The total of 168 forestry trial records was obtained, but only 129 records had precise geographic coordinates and trial outcome and could be used to validate model predictions. While sub-specific taxa can occupy different climatic niches (Thompson *et al.*, 2011), for simplicity and as naming was not consistent or verifiable, all species that had varieties or subspecies were grouped together (e.g. plantings of *Acacia longifolia* subsp. *longifolia* and *Acacia longifolia* ssp. *sophorae* were considered jointly as *Acacia longifolia*). Species with less than four trials were excluded from the experiment list. This gave fourteen Australian *Acacia* species with which to evaluate SDMs and the relative importance of variables in explaining the outcome of the forestry trials. The predictive power of SDMs was quantified for each species (n=14) found in forestry trials by calculating true skill statistic, sensitivity and specificity.

Southern African Plant Invaders Atlas (SAPIA)

This dataset contains records for over 700 naturalized and invasive species, with information on abundance, habitat preferences, time of introduction and distribution (Henderson, 1998). However, the analyses were restricted to Lesotho, South Africa and Swaziland as the other regions are relatively poorly sampled. The April 2012 version of SAPIA was used. The accuracy of predictive power of SDMs for each species (n=11) found in SAPIA was quantified by calculating sensitivity only as it is a presence-only dataset containing 10762 records of eleven species in question.

Modelling approach

The approach used in this study draws upon the most recent recommendations on correlative modelling of Australian *Acacia* species in literature with an aim of producing basic presence-absence models (Richardson *et al.*, 2011). Correlative models rely on strong, often indirect links between species distribution records and environmental predictor variables to make predictions (Robertson *et al.*, 2004). In this study native range absence records were not available of target taxon; as such presence-only data obtained from herbarium collections were used, despite their limitation, to develop models (Loiselle *et al.*, 2002; Funk & Richardson, 2002; Robertson *et al.*, 2004). While numerous approaches, with varying degree of success, have been used to develop the models that predict potential distribution of introduced species (Peterson, 2003; Gallien *et al.*, 2012), here a SDM approach that was quick to implement was chosen. Thus climatic suitability for species on the experiment list is estimated using four rainfall and temperature related variables (see detailed description of the variables on the next paragraph). The models were originally developed for 838 Australian *Acacia* species (Richardson *et al.*, 2011). The approach was slightly modified as the preliminary assessment study indicated that some of the species ranges were under-predicted when the exact approach was used.

For this study, the four 10-minute environmental variables were chosen based on their importance in *Acacia* ecology. These four variables were obtained from the WORLDCLIM database [www.worldclim.com (Hijmans *et al.*, 2005)]: annual mean temperature (Bio_1), maximum temperature of the warmest month (Bio_5), minimum temperature of coldest month (Bio_6), and annual precipitation (Bio_12). These variables were chosen from the nineteen available from WORLDCLIM, as they represent mean values and extremes (as species are limited by environmental extremes), and as other variables are highly correlated with one another (Nunez & Medley 2011). To reduce sampling bias only one occurrence record was retained per 10 minute grid cell for each species (for more details see (Richardson *et al.* 2011)).

2.2.2 Species distribution modelling

For each species, the minimum and maximum values were extracted from native range occurrence records for each predictor variable. These values were used to identify the range of values that each species could tolerate for each predictor variable. This approach minimises the effect of possible outliers that could have been present in the dataset due to misidentification errors (Richardson *et al.*, 2011). For each species, each of the four predictor variable maps were reclassified into a map consisting of presence (value = 1) and absence (value = 0). The resulting absence-presence maps were multiplied to generate final map indicating the range of climatic variability over which the species can survive (Guisan & Zimmermann, 2000). The model that was produced is equivalent to the marginal range of BIOCLIM but uses only four predictor variables (Nix, 1986). The analysis was conducted using the R statistical software (v. 2.11, R Development Core Team, 2010). The models were projected to southern Africa (Lesotho, South Africa and Swaziland) to identify regions climatically suitable for each species.

Evaluating model predictions

Guisan & Thuiller (2005) indicated that one of the challenges associated with using SDMs to predict species distributions is the assessment of the predictive accuracy. The availability of independent data sets enables the user to validate the predictive power of models and therefore their applicability in the management context. The relationship between predicted distributions and observed occurrences in southern Africa (forestry trials and SAPIA data) was evaluated using sensitivity, specificity and true skill statistic. Sensitivity is the proportion of observed presences predicted present and quantifies the omission error; and specificity is the proportion of observed absences predicted absent and quantifies commission error (Fielding & Bell, 1997). These measures range from 0 to 1 with 0 indicating no agreement between predicted and actual data and 1 indicating a perfect agreement. True skill statistic (TSS) includes omission and commission errors (Fielding & Bell 1997; Allouche *et al*., 2006). TSS takes into account both omission and commission errors and ranges from -1 to +1, where +1 indicates perfect agreement and values of zero or less indicates a performance no better than random. Allouche *et al.* (2006) indicated that TSS is a better measure compared to kappa statistics as it is not sensitive to prevalence.

2.2.3 Predicting the invasion risk

Occupancy of each species was calculated at the quarter degree grid cell (QDGC, 15 min. x 15 min.) level. Quarter degree grid cells covered by Australian *Acacia* species in southern Africa as obtained from SAPIA and forestry trials were used to estimate their current distributions. Species potential distribution was estimated based on climatic suitability and range size as the percentage of southern Africa (South Africa, Lesotho and Swaziland) predicted suitable by SDMs.

2.2.4 Factors that determine trial outcome

Unmistakably, other factors such as biotic interactions with the native communities, human influence, and ability to disperse could influence trial outcome at the local scale. I thus used a classification tree approach (Breiman, 1984) to test which factors (Table 2.1) determine outcome of species in historical plantings (Poynton, 2009). The list of explanatory variables included herbivory, invasiveness elsewhere, climatic suitability and biomes (see Table 2.1 for the 'coding' of each variable and justification why these variables were chosen)

Classification tree analysis

The classification tree was constructed by repeatedly splitting data, defined by a simple rule based on a single explanatory variable at each split. At each split, the data were partitioned into two exclusive groups, each of which was as homogeneous as possible (Breiman, 1984). An optimal tree was then determined by testing for misclassification error rates for the largest tree as well as for every smaller tree by ten-fold cross-validation constructed in CART Pro Ex v. 6.0. The software builds a nested sequence of branches by recursively snipping off the less important splits in terms of explained deviance. The length of the tree was controlled by choosing the one-SE rule, which minimizes cross-validated error within one standard error of the minimum cost tree rule (Pyšek *et al*., 2009).

Table 2.1: Descriptive variables relating to introduction outcome (trial success-species that survived and grew to maturity and failure-species that did not survive for long in trials) of Australian *Acacia* species in South African government forestry trials.

Variable	Criteria	Justification	Data sources
Trial outcome	0- failure (absence) 1-success (presence)		Poynton (2009)
Biotic	Did species fail because seeds were eaten by animals and birds? Coded as Y/N Y-yes N-no	Biotic factors have been indicated to influence survival that can lead to naturalization (Nuñez & Medley 2011)	Poynton (2009)
Climatic suitability	Coded as 0/1 0-Climate not suitable 1-Climate suitable	Climatic suitability is widely used to predict outcome of introductions McGregor *et al*., (2012a).	SDMs
Climatic variables	Coded as BIO-1, BIO_5, BIO_6, & BIO_12 Annual Mean temperature, Maximum Temperature of the Warmest Month, Minimum Temperature of the Coldest Month & Annual precipitation	Did trials succeed because of precipitation and temperature ranges? Castro-Díez *et al*., (2011)	Hijmans *et al*., (2006)
Biome	Given as names South African biomes	Were trials successful because of the biomes they were introduced to? Rouget *et al*., (2004)	Mucina & Rutherford (2006)
Invasiveness elsewhere	Coded as introduced, naturalized and invasive Invasiveness elsewhere according to Richardson *et al*., (2011)	Invasiveness elsewhere is one of the best predictors of the outcome of species introductions (Hulme, 2012)	Richardson *et al*., (2011)

2.3 Results

2.3.1 Species distribution modelling

The SDMs successfully predicted the introduction outcome of Australian *Acacia* species for all species lumped together as the overall sensitivity is 81(63%) of the 129 forestry records (overall TSS = 0.15, Table 2.2), with a high proportion of true presences predicted as present (sensitivity = 0.80) but a rather low percentage of true absences predicted as absent (specificity = 0.35). This indicates temperature and rainfall are determinants of trial outcome. However, there was higher proportion of false absences than false presences indicating that success was rarer than failure (Table 2.2).

Table 2.2: Relationship between climatic suitability (SDM predictions) and introduction outcome for forestry trial plantings; *a-true presences; b- false presences; c, false absences; and d, true absences;* Sensitivity (proportion of actual presences predicted as such); specificity (proportion of actual absences predicted as such); TSS (true skill statistic (*sensitivity + specificity-1*)..

Species	Number of sites	True presences (a)	False presences (b)	False absences (c)	True absences (d)	Sensitivity	Specificity	TSS
A. acuminata	13	1	5	1	6	0.50	0.54	0.04
A. aneura	4	1	1	2	0	0.33	0.00	-0.67
A.baileyana	5	4	1	0	0	1.00	0.00	0.00
A. cultriformis	5	0	2	1	2	0.00	0.50	-0.50
A. dealbata	13	11	0	1	1	0.91	1.00	0.91
A. decurrens	7	2	4	0	1	1.00	0.20	0.20
A. elata	9	2	4	2	1	0.50	0.20	-0.30
A. falciformis	4	2	2	0	0	1.00	0.00	0.00
A. longifolia	5	4	1	0	0	1.00	0.00	0.00
A. mearnsii	13	7	2	3	1	0.70	0.33	0.03
A. melanoxylon	28	20	8	0	0	1.00	0.00	0.00
A. pendula	6	1	1	2	2	0.33	0.67	0.00
A. pycnantha	9	7	1	1	0	0.88	0.00	-0.20
A. saligna	8	2	0	3	3	0.40	1.00	0.40
Overall	**129**	**64**	**32**	**16**	**17**	**0.80**	**0.35**	**0.15**

The results above indicate that climate-based SDMs are capable of producing predictions that accord well with invaded range data. Observed invaded ranges of Australian *Acacia* species in southern Africa are generally correctly predicted as suitable based on the SDMs (sensitivity = 0.87). However, the predictions mismatched 461 (13%) invasive range records, i.e. 13% of the records indicate that species invaded areas that are climatically unsuitable; Table 2.3. Most of the invasive species have the potential to substantially increase their ranges because more than half of southern Africa is predicted to be suitable.

Table 2.3: Relationship between climatic suitability (SDM predictions) and Southern African Plant Invaders Atlas data; a-true presences; c-false absence and Sensitivity (which is proportion of true presences predicted as such).

Species	Number of sites	True presences a	False absences c	Sensitivity
A. baileyana	86	82	4	0.95
A. cyclops	141	137	4	0.97
A. dealbata	717	707	10	0.99
A. decurrens	157	155	2	0.99
A. elata	20	17	3	0.85
A. longifolia	79	79	0	1.00
A. mearnsii	1916	1485	431	0.78
A. melanoxylon	163	163	0	1.00
A. podalyriifolia	56	51	5	0.91
A. pycnantha	83	82	1	0.99
A. saligna	53	52	1	0.98
Overall	**3471**	**3010**	**461**	**0.87**

The measures used to assess the relationship between SDM predictions and trial data indicate varied results between species, with five species having low sensitivity values and ten with low specificity values (Table 2.3). The results of model prediction, SAPIA and forestry plantings data for both widespread and abundant species in southern Africa (*Acacia dealbata* and *A. mearnsii*) shown in Fig. 2.1 indicate that SDMs were able to identify suitable ranges climatic for both species in southern Africa based on the chosen variables. However, the SDMs correctly predict regions of introduction but not the total current invaded ranges for some species, e.g. *A. mearnsii*, Fig. 2.1.

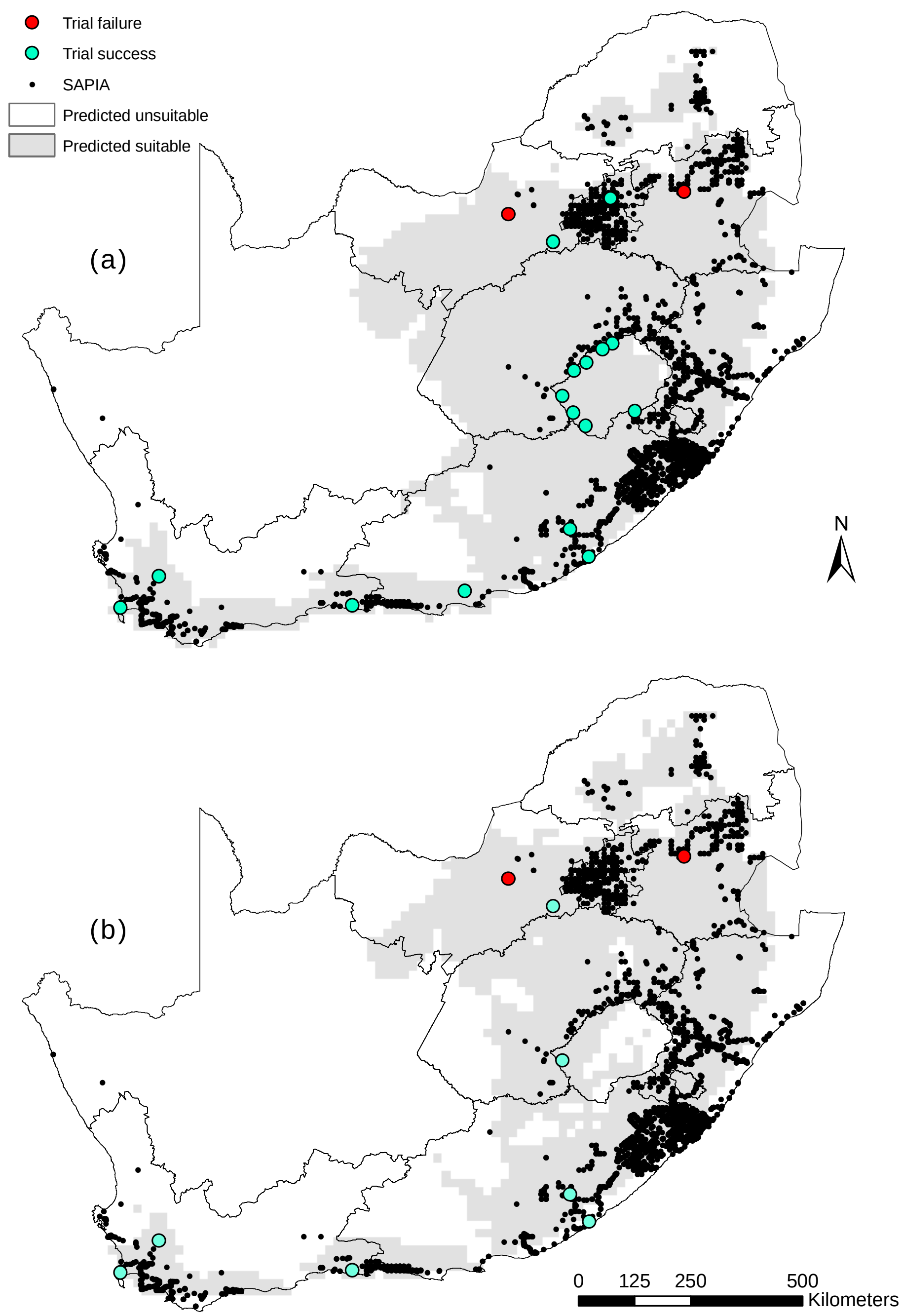


Figure 2.1: Model predictions overlaid with records of introduction outcome from historical trial plantings and invaded sites in Southern African Plant Invasion Atlas in South Africa, Lesotho and Swaziland–a) *Acacia dealbata* and b) *Acacia mearnsii.*

2.3.2 Explaining trial outcome

The relationship between introduction outcome and model predictions indicated that 81 of 129 trials (model accuracy = 0.63) were correctly predicted (Table 2.2), while 87 (model accuracy = 0.67) records were correctly predicted by the criterion "invasive elsewhere" (Fig. 2.2; Node 2 and 3). Based on the classification tree (Fig. 2.2), three variables (invasive elsewhere, annual mean temperature, and mean temperature of the coldest month) together accurately predicted 72% of the forestry trial records (i.e. 93 trials). The classification tree analysis correctly predicted forestry trial outcome significantly (sensitivity =0.86, specificity = 0.36 and TSS = 0.22).

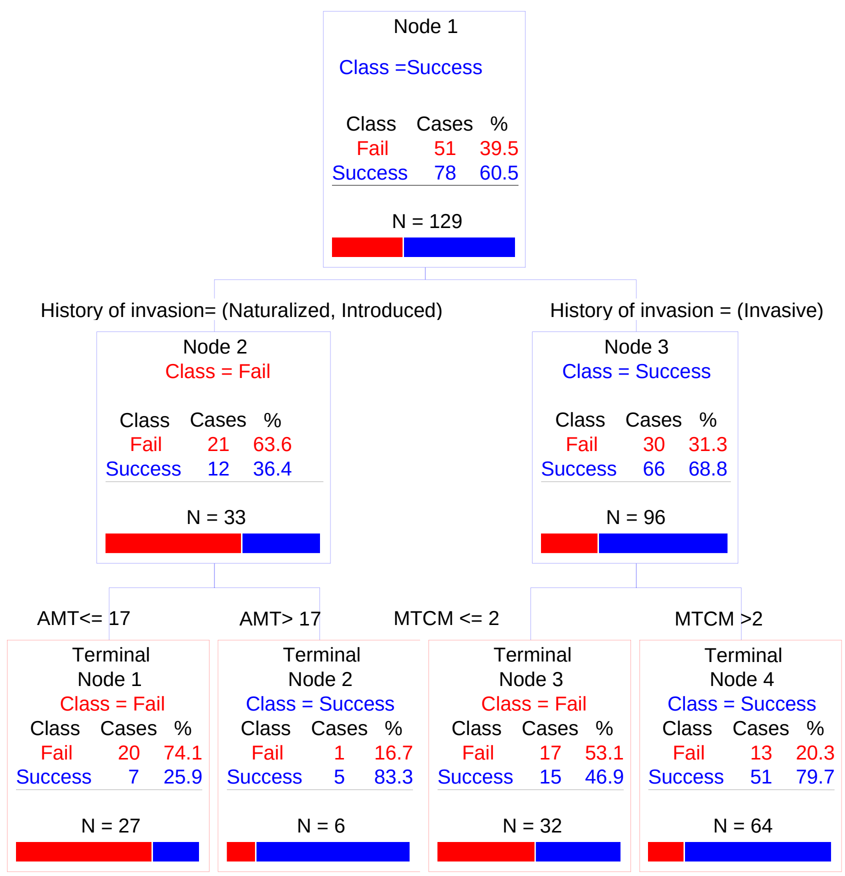


Figure 2.2: Classification tree analysis of the probability that Australian *Acacia* species will survive in trial (blue part of the bar) or not survive (red) based on various predictor variables (see Table 2). Each node shows a table for 'success' (species surviving in trials) or 'fail' (species that did not survive in trials) class, describing the number of cases in each class. Below the table is the total number of cases (N) and graphical presentation of the percentage of success and failure cases (horizontal bar). For each node the splitting criterion is written in caps on top of the nodes. Status is similar to invasiveness elsewhere and the two environmental variables: AMT-annual mean temperature and MTCM is minimum temperature of the coldest month.

2.3.3 Predicting an invasion risk

The wetter parts of the region (southern Africa) were identified as most suitable for the suite of Australian *Acacia* species analysed. SDMs predicted that thirteen species could become widespread. The following Australian *Acacia* species have large proportion of southern Africa as a climatically suitable range: *Acacia implexa*, *A. paradoxa, A. cultriformis*, *A. falciformis*, *A. pendula*, *A. rubida, A. stricta, A. retinodes*, *A. fimbriata*, *A. aneura*, *A. viscidula*, *A. acuminata* and *A. adunca* (Fig. 4). The remaining four species -*A. mangium*, *A. prominens, A. schinoides* and *A. binervata* appear to have a potential of localized extensive spread (Fig. 2.3). All of these species have not yet reached the full extent of climatically suitable ranges (See maps in Appendix I).

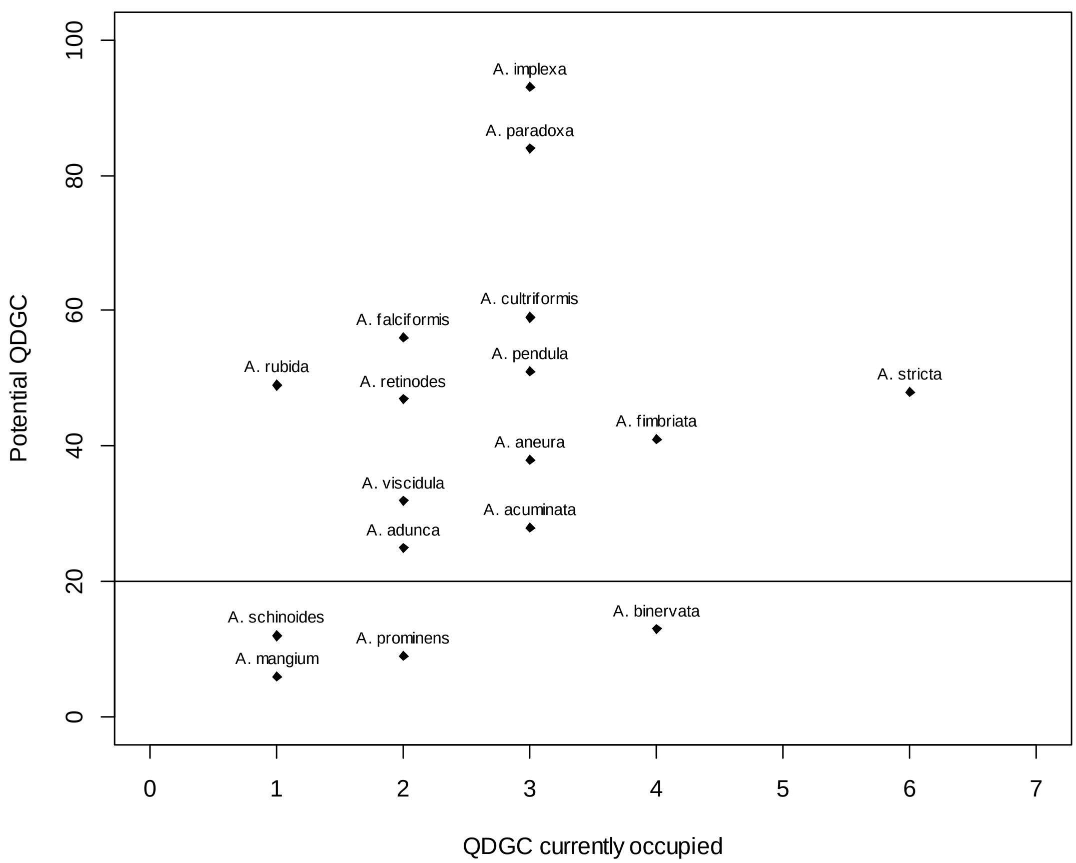


Figure 2.3: The percentage of southern Africa with climatically suitable ranges for Australian *Acacia* species that are not reported to be invasive ('non-invasive') based on SDM predictions expressed as 'potential QDGCs' (with a cut-off of 20% of southern Africa QDGCs climatically suitable) and QDGCs currently occupied per species compiled from both Southern African Plant Invaders Atlas and forestry trial plantings.

2.4 Discussion

2.4.1 Invasiveness of Australian *Acacia* species based on climatic suitability

The results show that climate-based models can predict sites where trials were successful (i.e. sites where species that were put in trials survived) and that forestry trial plantings data provide useful data for evaluating SDM predictions thereby identifying areas of introduction where species survived in trials. An overall proportion of presences that were predicted as presences (sensitivity =0.80; Table 2.2) indicate that models were capable of predicting 'trial success' (i.e. sites where trials were successful). McGregor *et al.* (2012a) stated that successful naturalization of pine species was linked to a good climate match between their native range and introduced ranges. The results emphasize the importance of climatic suitability for predicting tree invasions.

The fact that SDMs could not accurately predict failures of species suggests that climatic suitability provides a broad picture of where an introduced species might survive. However, factors such as biotic factors and other bioclimatic or environmental factors are as important in determining whether an introduced species will survive or not. This part of the study explained the ability of species to survive at certain sites or the inability thereof as only associated with climate variables related to temperature and rainfall. Factors such as seed predation, competition with local plants and herbivory are also key determinants of establishment or invasion success (Lake & Leishman, 2004).

The overall sensitivity value (0.87) indicates that climate-based SDMs could correctly predict areas invaded by Australian *Acacia* species in southern Africa. However, the SDMs could not correctly predict the currently invaded ranges (e.g. *A. mearnsii,* Fig. 2.1). Similarly, other studies (Broennimann *et al.*, 2007; Beaumont *et al.*, 2009) that explored predicting invasions indicated that SDMs calibrated based on native range records were able to predict region of introduction, but not the total invaded range indicating a possible niche shift. This suggests that species may alter its climatic niche during an invasion process. However, there is an on-going debate in literature about niche shift prevalence (Peterson, 2011). For example, Broennimann *et al.* (2009) indicated the evidence of niche shift for spotted Knotweed in North America and Europe while Martinez-Meyer *et al.* (2004) indicated that species maintain ancestral ecological requirements in different geographic area and time periods. According to the SDMs predictions in this study, even widespread species (e.g. *A. dealbata*) have not yet fully occupied all climatically suitable areas in southern Africa. However, management actions should be focused on containment; possible detection and removal of outlying populations of such species to avoid proliferation. For example, the management of pompom weed infestations in KwaZulu-Natal coast and the interior (Goodall *et al*., 2010).

2.4.2 High risk species

Australian *Acacia* species that are already introduced but not yet widespread are likely to spread to currently unoccupied climatically suitable ranges as SDMs predictions indicate that a large portion of southern Africa (Lesotho, South Africa and Swaziland) as suitable for invasion by 13 of the 17 currently introduced or naturalized (Fig. 4). This indicates that there is a major invasion debt and not simply an over-prediction in the SDMs, because there is a strong correlation between extent of usage and invasive distributions for Australian *Acacia* species in South Africa (Wilson *et al*., 2011). The widespread invaders are those species that have been planted for forestry, dune stabilization or ornamental purposes. However, many other introduced species can and do spread (Zenni *et al*., 2009; Kaplan *et al*., 2012). Species that have a large potential range and are invasive elsewhere (Fig. 2.3; Appendix I) should be prioritised for management, and where possible eradicated, e.g. *Acacia implexa*, *A. paradoxa* and *A. stricta* in South Africa.

2.4.3 Explaining trial outcome

In line with other studies, the results of this study indicate that the success of establishing species after introduction in the new range was greater for species recorded as invasive elsewhere (Scott & Panetta, 1993; Williamson & Fitter, 1996; Reichard & Hamilton, 1997; McGregor *et al*., 2012b). As such Australian *Acacia* species that established in trials appear to be a non-random subset of the global pool and tended to be species that are known to be invasive elsewhere and are within climatic areas similar to their native ranges are likely to invade large areas. Since Australian *Acacia* species that are known to be invasive elsewhere are already planted in southern Africa for forestry purposes (Richardson *et al*., 2011), their spread should be monitored so that they can be managed before they reach and invasion stage.

Commercial forestry is one of the major pathways to tree invasions (Essl *et al*., 2010) and availability of introduction data can be useful for screening potential invaders when used together with the SDMs. SDMs provide useful information that can influence management decisions on early detection and prioritization, and may facilitate targeted research that informs alien species management. SDMs also provide information for rapid, pre-border risk assessment of potential distribution of alien species.

The outcomes of this research can be used to inform policy and decision making processes regarding introduced Australian *Acacia* species. The first option is the detailed research focused on the risk assessment of species that are not reported to be invasive yet using this study as the baseline. Then the outcome from such studies will inform the process of listing species as part of the National Environmental Management Biodiversity Act 10 of 2004 (NEMBA) according to different categories by either Working for Water or SANBI ISP programmes. These programmes can also support research that includes field surveys at sites where species (excluding the widespread and abundant invasive species) were planted as part of the forestry trials. Such research would assess the current population dynamics and invasion risk based on the outcome of this study.

3 The occurrences of non-invasive Australian *Acacia* species in southern Africa: towards understanding their invasive status

Abstract

Introduced plant species that become invasive cause ecological and economical losses in their new ranges. Insufficient knowledge on the occurrences of introduced species in their new ranges prevents effective control and management of invading species. In this study, I explore the use of data from historical trial plantings together with other data sets that list introduced species in southern Africa (Lesotho, South Africa and Swaziland) using Australian *Acacia* species as the taxon of choice to determine current invasive status of species that are not known to be invasive ('non-invasive'). Occurrence data were obtained from various datasets and invasion biology experts. Species that were not well represented (i.e. with less than four records) were excluded from the list. Maps were generated to understand the occurrence patterns of the resultant nine species. Climatic suitability and invasiveness elsewhere data were obtained for each species. The study also focused on using collated data to conduct 'revisits' to determine the invasiveness of Australian *Acacia* species on the list. As it was not feasible to conduct revisits for all nine species, three ornamental species (*Acacia floribunda*, *A. pendula* and *A. retinodes*) were selected as part of the pilot study focusing on determining the current status of 'non-invasive' species thereby developing a protocol that can be used for surveying species at previously recorded sites. A total of 15 sites for *Acacia floribunda*, *A. pendula* and *A. retinodes* were revisited to determine the current invasive status. The results indicate that nine Australian *Acacia* species on the list could invade southern Africa as a large portion is predicted as climatically suitable and have been reported to have history of invading or forming naturalized populations elsewhere. This protocol is a rapid tool for investigating the spatial patterns and status of introduced Australian *Acacia* species. The protocol can be used to assess the invasive status of other taxa of woody plants.

Keywords: Field surveys, species invasive status, detection, forestry, Southern African Plant Invaders Atlas, expert knowledge, protocol

3.1 Introduction

Invasive alien species have gained increasing attention globally due to their substantial ecological and economic impacts. Mitigating or stopping the spread of emerging invaders needs data that list introduction sites of such species (*sensu* Mgidi *et al*., 2004). Emerging invaders are alien species with the potential to become problems without timely intervention (Mgidi *et al*., 2004). Agriculture, forestry plantations and horticulture contributed significantly to the intentional introduction of alien species into southern Africa (Poynton 1979a, 1979b, and 2009). Some of the intentionally introduced species became invasive (i.e. they produce offspring in large numbers that establish and form self-perpetuating populations at considerable distances from the parent plants (*sensu* Richardson *et al.*, 2000)). The use of alien tree species for human needs has contributed significantly to the economy of South Africa as a country, but there is a high cost associated with clearing well-established populations of invasive species introduced through these forestry activities (De Wit *et al.*, 2001; Le Maitre *et al.*, 2002).

Few Australian *Acacia* species have a significant impact on biodiversity and on natural vegetation (Richardson *et al*., 2011; van Wilgen *et al*., 2011) while others are not known as invasive in southern Africa. The differences in abundance and density of trees introduced into southern Africa can be explained by the extent and intensity of planting (van Wilgen *et al.*, 2011; Wilson *et al.*, 2011). This means species that were widely planted in large numbers are more abundant and widespread in the region (for example, *Acacia mearnsii* and *A. cyclops* in southern Africa). There is a need to determine the current invasive status of currently introduced species that are not yet invasive for management purposes, as the cost of managing invading species increases with the progression along the introduction-naturalization-invasion continuum (De Wit *et al*., 2001; Blackburn *et al*., 2011).

The studies that seek to quantify invasive status of already introduced species rely heavily on the availability of occurrence data in both the native and the introduced ranges and ideally such data should be complete and precise (McNeely *et al*., 2005; Meyerson & Mooney, 2007; Stoett, 2010). However, McGeoch *et al.* (2012) indicated that there are many challenges associated with data that lists introduced species in a new range. The challenges include among others the fact that the number of introduced species in the country is confounded by the amount of data available i.e. the distribution patterns observed are at least partly a consequence of data availability rather than the actual numbers of introduced species in a country (McGeoch *et al*., 2010). The collection and/or reporting of introduced species occurrences is biased as the collectors might be attracted to showy plants rather than inconspicuous species.

Here, the use of historical trial plantings data together with other datasets that lists Australian *Acacia* species introduced in southern Africa to understand current invasive status of non-invasive species was explored. For the sake of this study, non-invasive species means species that have not been recorded as invasive in southern Africa and the list includes species that either 'naturalized' or 'introduced' (Richardson *et al*., 2000; Blackburn *et al*., 2011). The historical trial plantings data provides information on the trial outcome for each species that was planted in southern Africa together with locations where trials were performed (Poynton, 1979a, 1979b, 2009). The trial outcome is given as either 'failure' (sites where species did not survive after planting) or 'success' (sites where species survived in trials) of species in different localities in southern Africa, making it feasible to conduct revisits in areas where trials were successful.

Surprisingly, little work has been done to determine the invasive status of populations of introduced Australian *Acacia* species at site level (but see Zenni *et al*., 2009; Kaplan *et al*., 2012). This gap is of particular concern for organizations that seek to manage invasions. To effectively manage or control invasions pro-actively, data on current invasive status together with potential range size estimated using species distribution models are essential (Wilson *et al*., 2014). This study was conducted in part to conduct 'revisits' following on the known occurrences of Australian *Acacia* species in southern Africa as an initial assessment of current invasive status. In this study, 'revisits' means conducting field surveys to search for species at previously known or recorded sites.

Wilson *et al.* (2013) proposed that initial assessment of current invasion status will help determine which strategies are needed and how much effort should be spent on management of target populations of alien plants. The basic current invasive status of the observed population can be determined by different metrics ranging from a basic current status to the impact that the species has, depending on the population dynamics of the observed populations (see Wilson *et al*., 2014). For example, the signs of recruiting populations indicate that there is a risk of population expansion that might lead to successful naturalization provided there are suitable sites for the target species (*sensu* Richardson *et al*., 2000). Recruiting populations are populations that reproduce offspring that survive to be added to a population (Richardson *et al*., 2000). Wilson *et al.* (2014) proposed it is important to determine the abundance and population growth rate for species that have recruiting populations.

This study is conducted in part, to determine the invasive status of non-invasive species using Australian *Acacia* species as the taxon of choice. The study uses a standardized set of metrics to assess and monitor tree invasions recommended by Wilson *et al.* (2014). Based on the recommended set of metrics, it is evident that their applicability depends on the expected outcome of each study; however this study focused on an initial basic status assessment. For example, the studies that seek to determine the likelihood of invasion by naturalized populations might focus on the abundance and population growth rate or extent and spread of the studied population. This study was focused on determining the current invasive status which included predicting the potential status of the introduced species based on climatic suitability. In addition, I conducted revisits to determine the abundance (number of individuals and estimated size and age) of located populations. The expected outcome of this task is characterization of three ornamental species according to the Blackburn *et al.* (2011) scheme.

Australian *Acacia* species are a good model group to understand current status of non-invasive species because the genus *Acacia* has many species that are introduced but are not yet invasive in southern Africa (Poynton 2009; Richardson *et al*., 2011). Currently, sixteen *Acacia* species are confirmed as invasive and five species are naturalized, but it is not clear whether the other 51 already introduced species are also likely to invade or not (Fig. 1.1; Richardson *et al*., 2011; Richardson & Rejmánek, 2011; Wilson *et al*., 2011). As it was not feasible to conduct revisits for all nine species on the list, I chose three ornamental species as part of the pilot study to determine the current invasive status based on observed populations. These ornamental species were selected because they were recorded in sites that are in close proximity to Pretoria.

The aim of this study was to determine the invasion status of Australia *Acacia* species that are introduced but not reported as invasive in southern Africa. This is done by outlining the steps taken to determine invasion status of Australian *Acacia* species, thereby categorising species into the unified framework scheme (Blackburn *et al*., 2011) following Wilson *et al.* (2014) recommendations on standardized set of metrics to assess tree invasions. I outline the steps taken from data collation to assigning invasive status during the process of determining target species invasive status. This can be used for future studies that will seek to determine the current invasive status of introduced species for effective control and management purposes following the protocol developed from this study.

3.2 Methods

3.2.1 Data compilation

The list of historical trial plantings of Australian *Acacia* species recorded in Tree Plantings in Southern Africa publication (Poynton, 2009) was used as a basis source of the dataset. Although this publication lists species planted in many African countries (Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia, and Zimbabwe), I restricted my dataset to South Africa, Lesotho and Swaziland as data for the target species are well represented. I expanded this dataset with data from other datasets that list introduced species in southern Africa that include: 1) Southern African Plant Invaders Atlas (SAPIA: L. Henderson pers. Comm.), 2) herbarium specimens (found in the section of 'cultivated plants' at the National Herbarium in Pretoria), 3) I-Spot (http://www.ispot.org.za/saving_species) and 4) the National Herbarium Computerized Information System (PRECIS) online database (http://posa.sanbi.org/intro_precis.php; accessed on June 2012 (Morris & Glen, 1978). Several invasion biology experts were consulted with respect to the sites where they have located *Acacia floribunda*, *A. pendula* or *A. retinodes* and data collated from these consultations is called 'expert knowledge' for this study.

SAPIA contains data on the distribution and habitat preferences for naturalized and invasive plants in southern Africa. Herbarium collections and PRECIS online database include data on date of collection, locality details (sites where species were observed either as street names or quarter degree grid cells) and whether the specimen was collected while the plant was flowering or fruiting. I-Spot is a website administered by South African National Biodiversity Institute (SANBI) that records organisms observed by the public. This data includes photographic, distributional and biographical information on observed taxa.

Data collated from these different sources were filtered to delete duplicates and nested records (e.g. PRECIS record similar to the one in SAPIA). The species that had fewer than four records were excluded from the list. For the resultant list with nine species, I confirmed the current known invasion status (i.e. introduced, naturalized or invasion stage *sensu* Blackburn *et al.* (2011) in southern Africa from Richardson *et al.* (2011). To understand the current observed occurrences of species on the list, occurrence maps were generated using ArcMap version 10.

3.2.2 Selection of species for revisits

In order to determine current invasive status of non-invasive Australian *Acacia* species, ornamental species were selected as part of the pilot study as it was not feasible to do the surveys for nine species listed as part of the experiment. Ornamental species were chosen as most recorded sites were in close proximity to Pretoria. Ornamental species have also been reported to have a capability of escaping from gardens and invade areas far from planting sites (Forsyth *et al*., 2004). Lockwood *et al.* (2009) indicated that repeated introductions aid successful establishments and more often ornamental species are repeatedly introduced in new ranges Pyšek *et al*. (2009). Information on the biology and general introductions data were necessary to plan the surveys for when plants are flowering and ascertain that these species have been introduced into southern Africa. The biology and general introductions data to different countries were recorded from the World Wide Wattle website (http://www.worldwidewattle.com/, accessed on 24 May 2012). This website compiles information from several sources of Australian national (including Flora of Australia) and regional flora information.

Biology of ornamental Acacia species

Acacia floribunda (Vent.) Willd. (White sally or gossamer wattle) is a leguminous tree that grows up to 8 m high, produces clusters of pale yellow flowers scattered on the rachis in June and September in the native range. It is endemic to forests and woodlands along the eastern and sub-coastal regions in Australia. This species is reported to have spread beyond its original native range within New South Wales and Queensland and has formed naturalized populations in New Zealand (www.anbg.au/abrs/online-resources/flora; accessed October 2012).

Acacia pendula A. Cunn.ex G. Don. (Weeping myall) is a leguminous tree that grows to up to 12 m in height. It is characterized by pendulous branches, produces sparse bright yellow flowers on peduncles within the leaf and branch axils in summer and autumn in Australia. It is endemic to the eastern parts of Australia from New South Wales to the semi-arid plains of Queensland (Orchard & Wilson, 2001). No information was available from the literature reporting an invasion of *Acacia pendula* in other countries.

Acacia retinodes Schldtl. (wirilda, swamp and silver wattle) is a leguminous tree that grows to a height of 10 m. Willis (1970) reported that there are two varieties of this species occurring in Australia namely *A. retinodes* var. *retinodes* and *A. retinodes* var. *uncifolia*. *Acacia retinodes* produces cream to yellow flowers and produces 15-30 flowers in each head in summer. *A. retinodes* var. *uncifolia* distribution is restricted to calcareous sand dunes while *A. retinodes* var. *retinodes* has a much wider inland distribution and is found as far south as Tasmania (Bernhardt & Walker, 1985). However, for the purpose of this study I grouped all the varieties together for simplicity. No information was available from the literature reporting an invasion of *Acacia retinodes* in other countries.

3.2.3 Revisits

Field surveys were conducted from July 2012 to March 2013. For each trip the time taken and distance travelled to the site from the University of Pretoria was recorded. To estimate the cost of conducting surveys, the University of Pretoria car hire rates (R/km) were used. The presence or absence of the target species at the visited site was recorded. Photos were taken at each site visited, specimens were collected and various variables related to the population dynamics at a given site were recorded (Table 3.1). The collected specimens and photos that were taken per site visit were used to verify species identity. In cases where the target plant was not found, the surroundings were searched for at least an hour.

Table 3.1: Data recorded during revisits at different sites used to assign the invasive status of located populations.

Variables	Description
General	
Date of survey	Date at which the survey was conducted
Area surveyed	Whether the area where the surveys were conducted was along the street or in a garden.
Plant name	Target species name
Target species presence/ absence	Can you see the plant?
Time spent searching	How much time did you spent searching at the vicinity
Number of trees per site	To estimate population size
Property ownership	Is the garden used by public or is it privately owned
Habitat-related	
Habitat description	A clear description of the site that is been sampled
Location points (Latitude and Longitude)	Coordinates of the site
Any form of disturbance	Any disturbances that interrupts the ecosystem processes e.g. soil disturbance or changes in fire regime
Plant-related	
Plant height	To estimate plant age
Circumference at knee level	To estimate plant age
Reproductive features	Does the tree have any seeds, flowers or fruits at the time?
Any recruitment signs	Does the species seem to recruit?

3.2.4 Assigning invasive status

To assign a status to the species on the list, I followed the recommendations in Wilson *et al.* (2014) by: 1) using the results obtained from field revisits; thus determining whether three ornamental species are spreading away from their introduction sites and forming self-sustaining populations and 2) characterizing species according to the unified framework scheme (Blackburn *et al.*, 2011) given as Appendix II.

Species distribution modelling and invasiveness elsewhere

To predict the potential status of species on the list, climate-based species distribution models that were generated for chapter 2 were used. The same modelling approach as in chapter 2 was followed. Then the relationship between model predictions and species occurrence data on the list were assessed by calculating sensitivity (Fielding & Bell 1997). The current invasiveness elsewhere data were obtained from a recent publication on global introductions of Australian Acacia species (Richardson *et al.*, 2011).

3.3 Results

3.3.1 Collated data

A total of 124 records were collated from different sources for species on the list, of which 90 (73%) could be used for revisits. Of the 90 records that could be used for revisits, forestry trials contributed 44%, while a combination of specimens and records from the PRECIS online database contributed 42%, and expert knowledge and SAPIA contributed 14%. Collected data indicate that there are many Australian *Acacia* species that are introduced into South Africa for which the current status has not been assessed (Table 3.2).

Table 3.2: Data of Australian *Acacia* species that are already introduced into southern Africa but are not reported to be invasive including total number of sites per species, sites with precise localities that can be used for revisits and the data sources where the data was obtained (*Acacia floribunda*, *A. pendula* and *A. retinodes* were selected for conducted revisits in this study).

Species	Total number of sites	Sites with precise localities	Sites recorded in SAPIA	Sites for forestry trial plantings	Sites in Specimens & Pretoria Computerized Information system	Sites from experts
A. acuminata	13	13	0	13	0	0
A. adunca	5	3	2	1	0	0
A. aneura	10	7	0	5	2	0
A. cultriformis	30	23	1	8	10 + 4	0
A. falciformis	6	4	0	4	0	0
A. fimbriata	14	12	1	1	7 + 3	0
A. floribunda	10	9	0	0	2	7
A. pendula	26	15	0	8	5	2
A. retinodes	9	5	0	0	5	0
Total	**124**	**90**	**4**	**39**	**38**	**9**

Non-invasive Australian *Acacia* species in southern Africa

The results indicate that southern African is likely to be invaded by nine Australian *Acacia* species on the experiment list as a large portion of the country is predicted to be suitable. Predicted climatic suitability also indicates that nine species occur in climatically suitable areas while there is a large portion of the region with climatically suitable range not yet occupied. Maps of the recorded occurrences and predicted suitability of *Acacia cultriformis* and *A. fimbriata* are provided as examples (Fig. 3.1). The top five species for which most records were available include *Acacia cultriformis*, *A. pendula*, *A. fimbriata*, *A. acuminata*, and *A. floribunda* (Table 3.2).

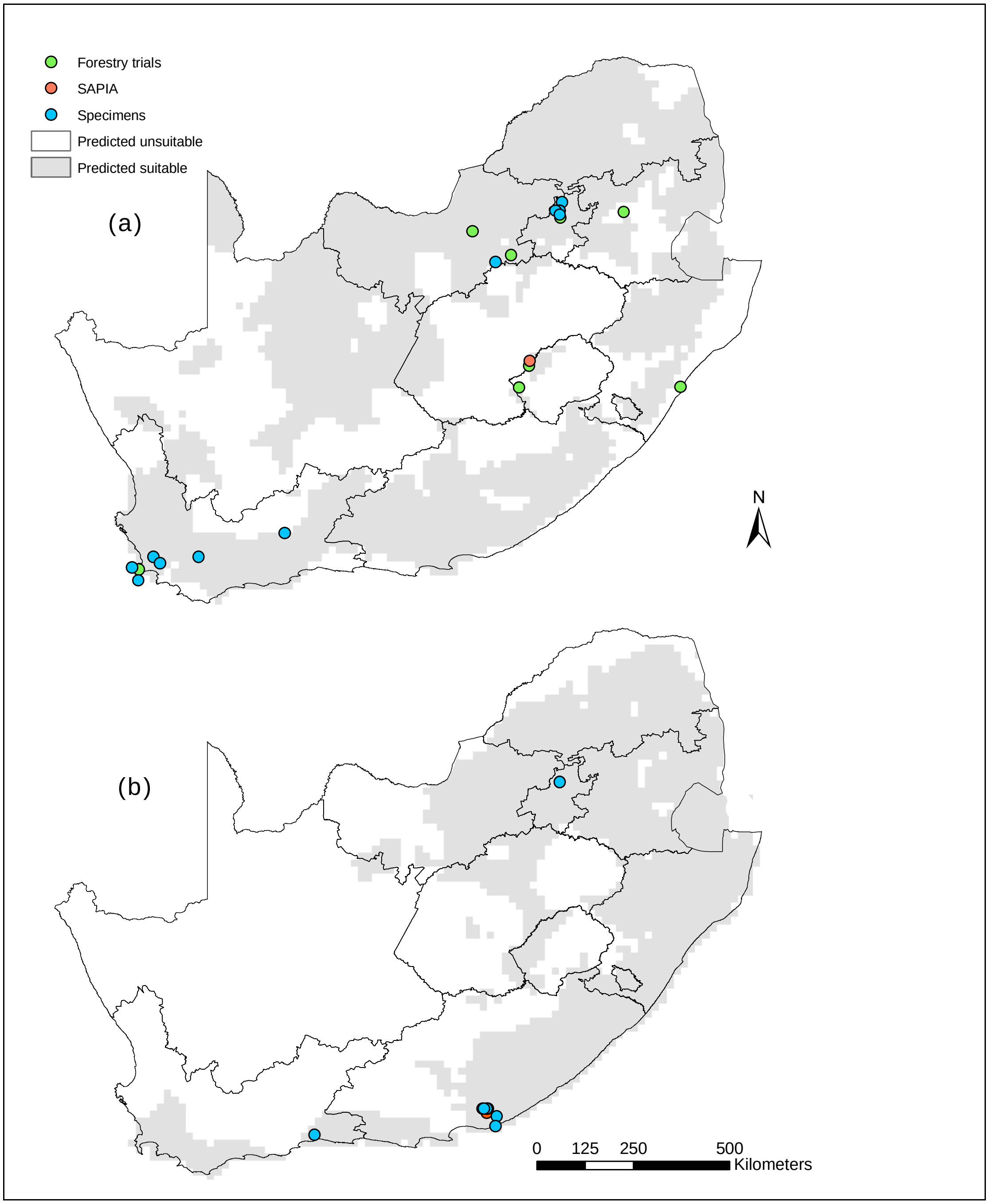


Figure 3.1: Model predictions overlaid with records of introduction outcome from historical trial planting data ‘trial success’ and red circles-sites where species did not survive in circles called ‘trial failure’) and invaded sites in SAPIA in South Africa, Lesotho and Swaziland)–a) *Acacia cultriformis* and b) *Acacia fimbriata.*

3.3.2 Revisits

Estimated cost

Trips that were conducted in South Africa to search for *Acacia pendula*, *A. retinodes* and *A. floribunda* cost approximately ZAR 2557.38 (Table 3.3). The amount of money that was spent for revisits ranges from ZAR 10 to 952.90, depending on how far the site was from the University of Pretoria (Table 3.3).

Table 3.3: Costs associated with conducting revisits of three ornamental species in South Africa. Distance indicates the kilometers that were covered per trip while time indicates time taken to reach the destination from University of Pretoria and time spent to search in the vicinity of the recorded sites was recorded. The total number of localities and cost of trip were recorded.

Trip	Distance (km)	Time (hours)	No of localities visited	Cost of trip (ZAR)
Pretoria-Springs-Heidelberg-Pretoria	330.1	4	2	429.13
Pretoria-Agricultural Research Council-Pretoria	50.4	3	1	65.52
Pretoria-University of Witwatersrand-Emmarentia Johannesburg Botanic Gardens-Krugersdorp-Pretoria	201.1	4	3	261.43
Pretoria-Lichtenburg-Potchefstroom-Pretoria	630	10	2	819.00
Pretoria-Capital Park-Ermelo-Pretoria	733	12	2	952.90
Pretoria-university of Pretoria's Experimental Farm-Pretoria	8	0.5	1	10.40
.1	30	1	1	39.00
Total	**1982.6**	**34.5**	**12**	**2577.38**

Located populations

Of the twelve sites that were visited, ornamental species populations were located at six sites (Fig. 3.2). Collected specimens were lodged at two herbaria (South African National Biodiversity Institute and University of Pretoria). The records that were not located were old records from herbarium specimens and those where coordinates were obtained using Google earth. For example, the specimen record indicated that *Acacia floribunda* trees were located at the Johannesburg Botanical Gardens in Emmarentia in 1977 although they could not be found during the revisit. *Acacia retinodes* was recorded to have been observed at the Agricultural Research Council-Vegetable and Ornamental Plant Institute (formerly known as Roodeplaat Horticultural Research Institute) in 1949. After a thorough search within the ARC institute the *Acacia retinodes* plants were not found

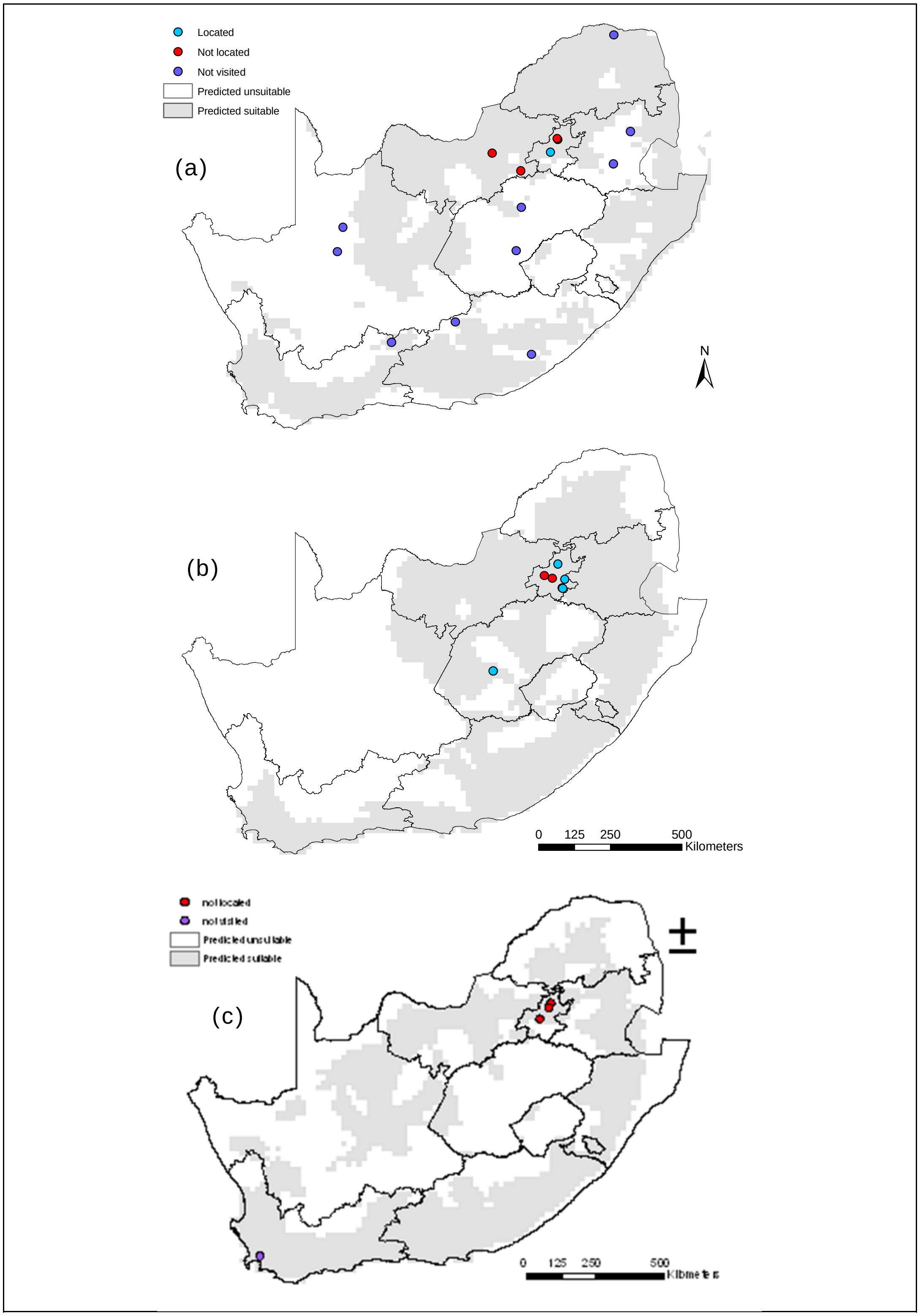


Figure 3.2: Surveys conducted for ornamental species (*Acacia pendula*, *A. floribunda* and *A. retinodes*). Sites that were not visited are given as "not visited" while populations that were found are "located" and the populations that were not found are "not located".

3.3.3 Invasion status of ornamental species based on observed populations

Based on data collected from revisits and the literature, three ornamental species (*Acacia pendula*, *A. floribunda* and *A. retinodes*) can be characterised based on Blackburn *et al.* (2011) scheme following Wilson *et al.* (2014) recommended set of metrics. An observed population of *Acacia pendula* at at the Johannesburg botanical garden (Emmarentia) with young pods indicates that this species can produce seeds. Based on this result, I propose characterising *A. pendula* as species that produces flowers but no seedlings (C2) on the Blackburn *et al.*, (2011) scheme. The observed population of *Acacia floribunda* had no pods but trees had galls and old flowers and the proposed status of this species is 'species that flower but do not produce viable seeds' (C1) on the scheme. No *Acacia retinodes* populations were seen during the revisits of recorded sites. The incorporation of climatic suitability and invasiveness elsewhere indicates that all species are likely to invade the region as the large proportion of the country is predicted to be suitable and these species are reported to be invasive elsewhere (Richardson *et al.*, 2011)

3.4 Discussion

3.4.1 Non-invasive species occurrence data

Data listing introduced Australian *Acacia* species provided a valuable source of data for understanding invasions as part of this study. Similarly, studies have used data sources that list species in their introduced ranges like herbarium collections to understand invasions (Barney *et al*., 2008; Aikio *et al*., 2010). Several other invasion biology studies in southern Africa used datasets like SAPIA, PRECIS and herbarium collections to understand invasions (Nel *et al*., 2004; Rouget *et al*., 2004; Wilson *et al*., 2007). There are both temporal and geographic biases associated with the use of such data for understanding invasions (Graham *et al*., 2003; McGeoch *et al*., 2010). A temporal bias may be present because of irregular collecting intensity. Collection intensity can differ as collectors of plants might be attracted to showy plants and these are more noticeable than inconspicuous species (Barney, 2006). The analysis based on the collated data can potentially underestimate the current actual distribution of the target species and thus underestimate the invasion risk, but these data represent a useful starting point.

Data that records the spatial and temporal distribution of introduced species in their new range is important as management needs such data in order to pro-actively manage potential invaders (Wilson *et al*., 2014). For example, Wilson *et al.* (2014) proposed that herbarium records should be used as evidence for the presence of target species in the area and then based on such data revisits can be conducted to assess the current invasive status of the target species. The results can help management to avoid reacting to species that are already widespread, and open an opportunity of strategically planning and choosing best-suited management options.

3.4.2 Overview of non-invasive Australian *Acacia* species in southern Africa

The spatial pattern of already introduced, non-invasive species on the experiment list for this study indicates some of these species are widely planted in different parts of southern Africa. Based on the collated data, the most frequently planted species are *Acacia cultriformis*, *A. fimbriata* and *A. pendula* (Fig. 3.3). However, the collated data for nine Australian *Acacia* species in fig. 3.3 include sites with no precise geographic localities; as such it is not feasible to conduct revisits for such records in the future. Lockwood *et al.* (2009) indicated that species that are most likely to invade are those that are most frequently planted in the introduced range. This means that there is a need for a detailed study focusing on assessing the invasion risk of these species on the experiment list. The need of such studies is evident as Australian *Acacia* species like many taxa are reported to undergo a lag phase before they are observed to invade (Wilson *et al*., 2011). The outputs of these studies will guide proactive management of introduced species that are likely to invade the region. This will help to maximize the efficiency of resources allocated for management of introduced taxa.

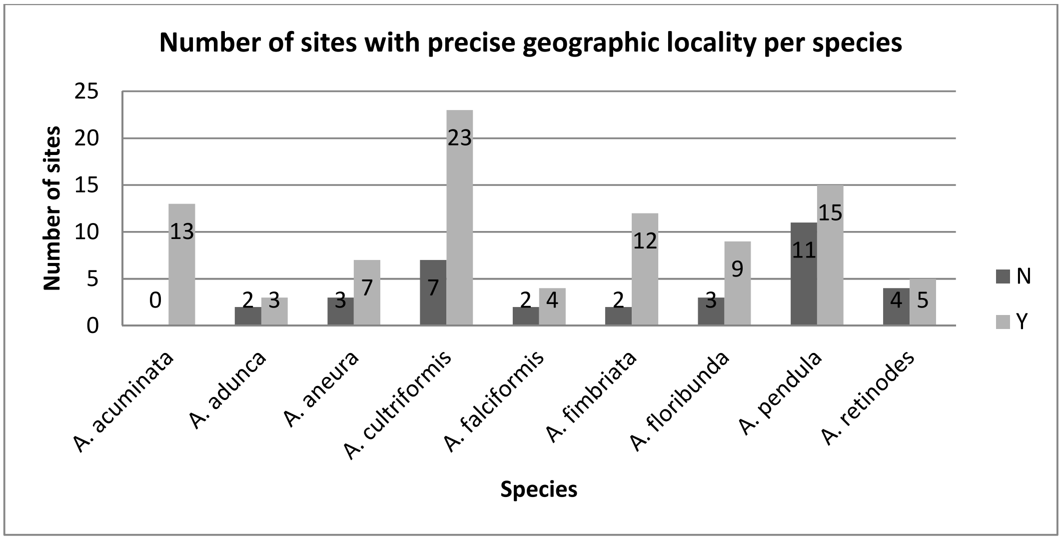


Figure 3.3: Non-invasive Australian *Acacia* species in southern Africa, data collated from SAPIA, PRECIS online database, herbarium collections, historical trial plantings and I-Spot. This figure indicates whether collated data had a precise geographic locality (Y) and or not (N).

3.4.3 Invasion status of three ornamental species

Acacia floribunda

The proposed invasion status of *A. floribunda* based on the results of this study is: 'individuals surviving in the wild in location where introduced, no reproduction, (C1)' in Blackburn *et al.* (2011), given as Appendix II in this study. The individuals of this species had galls on them indicating that there is a biological agent feeding on them and no seeds were observed. Literature indicated that *Acacia floribunda* is attacked by a galling wasp (*Trichilogaster Acaciaelongifoliae*) that was intentionally introduced in South Africa as a biological control agent of *Acacia longifolia* (Dennill *et al.* 1993). Marchante *et al.* (2011) indicated that *T. Acaciaelongifoliae* was collected from both *Acacia floribunda* and *A. longifolia* in Australia. Noble (1940) indicated the agent as the galling wasp on the flower buds of *Acacia floribunda*, *A. longifolia* and *A. sophorae*. The presence of the wasp is evident in South Africa, but there is a need verify the species identity.

Acacia pendula

It is not easy to characterize the observed populations of *A. pendula* based on the results of this study as the seed viability study was not conducted. I propose the status C2 (i.e. individuals survive in the wild in the location where introduced, reproduction occurring but population not self-sustaining) on Blackburn *et al.* (2014) scheme (Appendix II). The observed trees had pods on them and this indicates the possibility of the species reproducing.

This species is planted in a botanical garden and there is a possibility that seedlings might be pulled out to keep mature plants only, so I am cautiously interpreting 'not self-sustaining' as the species might be self-sustaining in an uncontrolled environment. All species were planted in the gardens or along the streets, so there is a possibility that growing seedlings are being pulled out regularly by land owners or that seedlings are unable to establish in highly managed areas (such as regularly mowed lawns). However, literature indicated that the South African National Biodiversity Institute Invasive Species programme (SANBI ISP) proposed this species for inclusion in the National Environmental Management Biodiversity Act 10 of 2004 (NEMBA) as a Category 3 weed (Wilson *et al.*, 2013). Category 3 plants are invasive species regulated by activity. An individual plant permit is required to import, possess, grow, breed, move, sell, buy or accept as a gift involving a Category 3 species. No permits will be issued for Category 3 plants known to exist in riparian zones. The records do not indicate the introduction of biological control introduced for *A. pendula* in southern Africa.

Acacia retinodes

No populations of *A. retinodes* were observed during the revisits and the species cannot be assigned to any Category. The literature indicated that SANBI ISP proposed this species for inclusion as a National Environmental Management Act (NEMBA) Category 1a weed (Wilson *et al.*, 2013). The Category 1a species are invasive species that require compulsory control by law to be removed or destroyed (eradicated) from the environment and no permits will be issued for propagation or sale. It is currently targeted as part of an eradication attempt at Tokai Arboretum in Cape Town (Wilson *et al.*, 2013). There are no records of biological control agents introduced for *A. retinodes* in southern Africa.

3.5 Recommendations

The methods followed in this study provide a protocol that is a foundation for conducting revisits for introduced species to determine invasion status at a local scale. The reliable application of this protocol to a large number of local projects will facilitate risk assessments for species that are already introduced in an area. Although the protocol was developed for Australian *Acacia* species, it can be adapted for use in assessment of all other plant taxa introduced into southern Africa. Once this approach is implemented across a representative range of species, it will be possible to determine the appropriate current invasive status and can be used as a method that leads to quantifying the abundance of observed populations. Ultimately, revisits will be used to detect new invaders, thereby leading to strategic planning and choice of suitable management actions. This means that it may also be possible to establish a range of possible eradication or containment projects in the region that will lead to efficient pro-active management strategies by using the adapted protocol (see Wilson *et al*., 2013).

With the current rate at which invasions increase in southern Africa, it would be prudent to invest greater resources into detection of new invaders by conducting revisits. Wilson *et al.*, (2013) proposed that revisiting introduced species at the previously known sites may provide information that will help management of potential invasions. Wilson *et al.* (2014) provides the needed standardized set of metrics of assessing and monitoring tree invasions. These metrics are linked to the Blackburn *et al.* (2011) unified framework, making it possible to assign species into current invasion status and gives decision and policy-makers baseline data to plan management per target species. This protocol can serve as a standardized procedure for 'revisits' and can be adapted if necessary to a more suitable option per project. Australian *Acacia* species are among the top three invasive genera in southern Africa, and are the well-studied group with introductions data available making it feasible to understand invasions. The developed protocol can be regarded as relatively quick, simple, cost-effective and reliable method for detecting new invaders and assessing current invasive status of an introduced species.

4 Summary and Conclusion

To my knowledge, this is the first study using historical trial plantings data to understand Australian *Acacia* invasions in southern Africa. This is important because Australian *Acacia* species that were introduced for (agro) forestry purposes were not a random sample from the species pool but actually possess characteristics that are also associated with a tendency to become invasive (Richardson *et al*., 2011). Kull *et al.* (2011) indicated that Australian *Acacia* as an important group in terms of forestry, ornamental gardening and landscape architecture, while Wilson *et al.* (2011) indicated that this taxon is reported as being among the worst invaders in southern Africa and other parts of the world. Several Australian *Acacia* species have become invasive in southern Africa and a third of resources allocated on clearing invaded stands is spent on this taxon (van Wilgen *et al*., 2011). Several other species introduced into southern Africa remain in small populations within limited ranges (van Wilgen *et al*., 2011, Wilson *et al*., 2011; Zenni *et al*., 2009) as such this taxon is an ideal subject for invasion risk assessment studies.

This thesis presents the results from two post-border risk assessment studies on Australian *Acacia* species introduced into southern Africa. Post-border risk assessment deals with species that are already introduced into the new range and aims to assess invasion risk (Wilson *et al*., 2013). There is a need to assess the invasiveness of introduced species for management purposes. Wilson *et al.* (2014) indicated that there is a real danger of responding to naturally viable populations that ultimately fail to invade (Simberloff & Gibbons, 2004; Zenni & Nunez, 2013). This thesis was conducted in part to differentiate between species that are likely to invade based on SDM predictions and history of invasion elsewhere as well as the initial assessment of current invasive status of non-invasive species based on literature and by revisiting sites where they were reported to be growing. Studies like mine allow the inference of common hypotheses associated with invasions (Hayes & Barry, 2008; van Kleunen *et al*., 2010) and result in the formulation of different biogeography hypotheses that unify the historical patterns of introduced species in space and time.

4.1.1 Climatic suitability and history of invasion

The first component of this study was conducted in part to understand why some species did not survive ('trial failure') while others survived ('trial success') in historical trial planting using climate-based SDMs. Results indicate that trial outcomes (i.e. failure or success) can be explained by climatic suitability and a history of invasion elsewhere (Table

2.2; Fig. 2.2 Chapter 2). These results further support the hypothesis that climatic suitability and a history of invasion elsewhere are key factors that can be used to predict invasions (Hayes & Barry, 2008; van Kleunen *et al.*, 2010; Nuñez & Medley, 2011). Climatic suitability and invasiveness have also been highlighted in several studies as predictors of species success at any stage of the introduction-naturalization-invasion continuum (Essl *et al.*, 2010; Essl *et al.*, 2011b; McGregor *et al.*, 2012b; Richardson & Pyšek, 2012). For example, climatic suitability was indicated to be a predictor of both pine naturalizations and invasions (McGregor *et al.* 2012a, Essl *et al.* 2011; Nuñez & Medley, 2011).

The results also indicated that climate-based model predictions did not successfully predict forestry trial failures (Table 2.2; Chapter 2). This might be explained by the fact that climate only sets the broad parameters for determining if an area is suitable for species to occur. Climatic suitability does not account for all interactions occurring between introduced species and biotic factors. For example, Nuñez *et al.* (2011) study also found that the presence of natural enemies can be one factor that explains the pine invasion failures, so factors other than climate might have caused Australian *Acacia* species not to survive in trials.

Model predictions indicated that many more Australian *Acacia* species could invade southern Africa as there are climatically suitable ranges for these species. This means that there is still a need for detailed studies focusing on this taxon. Such studies should explore the use of the standardized set of metrics for assessing tree invasions as proposed by Wilson *et al*., (2014). Wilson *et al.* (2014) proposed that a set of metrics should include information on current status, abundance, spatial extent, and impact of an invasion and how these characteristics change through time. Based on the focus of the study, the set of metrics will help to ultimately place species into management and legislative categories hence strategic planning process for management (Wilson *et al*., 2014).

4.1.2 Overview of non-invasive species in southern Africa

The second component focused on determining the invasiveness of Australian *Acacia* species that are already introduced into southern Africa but are not reported to be invasive ('non-invasive' species). To determine the invasiveness of these species, data collated from different data sources that list introduced species in southern Africa were used to conduct revisits at known localities of the species. The results indicated *Acacia cultriformis*, *A. pendula* and *A. fimbriata* as the most frequently recorded species in the region. As such there is a need for detailed studies that assess and monitor the spread of these species in southern

Africa, so that necessary management action can be taken. This will increase benefits associated with early detection in management of invasions (Wilson *et al*., 2013).

4.1.3 Invasion status of ornamental species and protocol

The observed populations of *Acacia floribunda* had a biological control agent feeding on them, but it was out of the scope of this thesis to determine if the biological control agent was *Trichilogaster Acacialongifoliae* as proposed in literature (Noble 1940, Dennill *et al*., 1993; Marchante *et al*., 2011). This indicates the need for a further research to determine the identity of the species. Based on literature, *Acacia pendula* is proposed for inclusion as a Category 3 weeds according to NEMBA Act 10 of 2004 by SANBI ISP (Wilson *et al*., 2013). This means that there will be work done to monitor the spread of observed populations of this species as reported in literature as proposed in Wilson *et al.* (2013). There is also a need for seed viability studies on a population of *Acacia pendula* observed in the Johannesburg Botanical Garden. *Acacia retinodes* has also been proposed for listing as a Category 1a species according to NEMBA Act 10 of 2004. The literature also indicates that there is an attempt to eradicate this species at Tokai Arboretum (Wilson *et al*., 2013).

Finally, a useful extension of this research would be to further conduct revisits for species already introduced into southern Africa to determine the current invasion status, abundance and population growth, extent and spread, and finally impacts and threats posed following recommendations in Wilson *et al.* (2014). This will help in initial assessment of invasion risk and lead to effective pro-active management. Then, all revisits conducted coupled with information on climate suitability and invasion elsewhere can be used to predict species invasiveness in southern Africa. This will fulfil the requirement for the initial steps in the management of introduced species (Wilson *et al*., 2013; 2014).

5 References

Aikio, S., Duncan, R.P., & Hulme, P.E. (2010) Herbarium records identify the role of longdistance spread in the spatial distribution of alien plants in New Zealand. *Journal of Biogeography*, **37**, 1740-1751.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223-1232.

Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M (2005) Validation of species-climate impact models under climate change. *Global Change Biology*, **11**, 1504-1513.

Baker, H. (1986) Patterns of plant invasion in North America. *Ecology of biological invasions of North America and Hawaii*, Springer. 44-55 pp.

Barney, J.N. (2006) North American history of two invasive plant species: phytogeographic distribution, dispersal vectors, and multiple introductions. *Biological Invasions*, **8**, 703-717.

Barney, J.N., Whitlow, T.H. & Lembo A.J. Jr. (2008) Revealing historic invasion patterns and potential invasion sites for two non-native plant species. *PLoS ONE*, **3**, e1635.

Beaumont, L.J., Gallagher, R.V., Thuiller, W., Downey, P.O., Leishman, M.R. & Hughes, L. (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions*, **15**, 409-420.

Bernhardt, P. & Walker, K. (1985) Insect foraging on *Acacia retinodes* var. *retinodes* in Victoria, Australia. *International journal of entomology*, **27**, 97-101.

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U. & Richardson, D.M. (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, **26**, 333-339.

Breiman, L., Friedman J, Olshen R & Stone C (1984) *Classification and Regression Trees*, Wadsworth.

Breton, C., Guerin, J., Ducatillion, C., Médail, F., Kull, C.A. & Bervillé, A. (2008) Taming the wild and 'wilding' the tame: Tree breeding and dispersal in Australia and the Mediterranean. *Plant Science*, **175**, 197-205.

Broennimann, O. & Guisan, A. (2008) Predicting current and future biological invasions: Both native and invaded ranges matter. *Biology Letters*, **4**, 585-589.

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701-709.

Carlton, J.T. (1996) Biological Invasions and Cryptogenic Species. *Ecology*, **77**, 1653-1655.

Castro-Díez, P., Godoy, O., Saldaña, A. & Richardson, D.M. (2011) Predicting invasiveness of Australian *Acacia* species on the basis of their native climatic affinities, life history traits and human use. *Diversity and Distributions*, **17**, 934-945.

Coetzee, B., van Rensburg, B. & Robertson, M. (2007) Invasion of grasslands by silver wattle, *Acacia dealbata* (Mimosaceae), alters beetle (Coleoptera) assemblage structure. *African Entomology*, **15**, 328-339.

Daehler, C.C., Denslow, J.S., Ansari, S. & Kuo, H.C. (2004) A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. *Conservation Biology*, **18**, 360-368.

De Wit, M., Crookes, D. & van Wilgen, B. (2001) Conflicts of interest in environmental management: estimating the costs and benefits of a tree invasion. *Biological Invasions*, **3**, 167-178.

Dennill, G., Donnelly, D. & Chown, S. (1993) Expansion of host-plant range of a biocontrol agent *Trichilogaster Acaciaelongifoliae* (Pteromalidae) released against the weed *Acacia longifolia* in South Africa. *Agriculture, Ecosystems & Environment*, **43**, 1-10.

Elith, J. & Leathwick, J.R. (2009) Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution and systematics*, **40**, 677-697.

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Hülber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I. & Nentwig, W. (2011a) Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences*, **108**, 203-207.

Essl, F., Mang, T., Dullinger, S., Moser, D. & Hulme, P.E. (2011b) Macroecological drivers of alien conifer naturalizations worldwide. *Ecography*, **34**, 1076-1084.

Essl, F., Moser, D., Dullinger, S., Mang, T. & Hulme, P.E. (2010) Selection for commercial forestry determines global patterns of alien conifer invasions. *Diversity and Distributions*, **16**, 911-921.

Ficetola, G.F., Thuiller, W. & Miaud, C. (2007) Prediction and validation of the potential global distribution of a problematic alien invasive species - The American bullfrog. *Diversity and Distributions*, **13**, 476-485.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38-49.

Forsyth, G., Richardson, D.M., Brown, P. & van Wilgen, B.W. (2004) Rapid assessment of the invasive status of Eucalyptus species in two South African provinces. *South African Journal of Science*, **100**, 75-77.

Funk, V.A. & Richardson, K.S. (2002) Systematic data in biodiversity studies: use it or lose it. *Systematic Biology*, **51**, 303–316.

Gaertner, M., Den Breeyen, A., Hui, C. & Richardson, D.M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography*, **33**, 319-338.

Gallagher, R.V., Leishman, M.R., Miller, J.T., Hui, C., Richardson, D.M., Suda, J. & Trávníček, P. (2011) Invasiveness in introduced Australian *Acacia* species: The role of species traits and genome size. *Diversity and Distributions*, **17**, 884-897.

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N.E. & Thuiller, W. (2012) Invasive species distribution models - how violating the equilibrium assumption can create new insights. *Global Ecology and Biogeography*, **21**, 1126-1136.

Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford University UK.

Gibson, M.R., Richardson, D.M., Marchante, E., Marchante, H., Rodger, J.G., Stone, G.N., Byrne, M., Fuentes-Ramírez, A., George, N., Harris, C., Johnson, S.D., Roux, J.J.L., Miller, J.T., Murphy, D.J., Pauw, A., Prescott, M.N., Wandrag, E.M. & Wilson, J.R.U. (2011) Reproductive biology of Australian *Acacia* species: Important mediator of invasiveness. *Diversity and Distributions*, **17**, 911-933.

Goodall J., Witkowski, E.T.F., Ammann, S. & Reinhardt, C. (2010) Does Allelopathy explain the invasiveness of *Campuloclinium macrocephalum* (pom pom weed) in South African grassland biome. *Biological Invasions*, **12**, 3497-3512.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147-186.

Hayes, K.R. & Barry, S.C. (2008) Are there any consistent predictors of invasion success? *Biological Invasions*, **10**, 483-506.

Henderson, L. (1998) Southern African Plant Invaders Atlas (SAPIA). *Applied Plant Science*, **12**, 31-32.

Henderson, L. (2007) Invasive, naturalized and casual alien plants in southern Africa: A summary based on the Southern African Plant Invaders Atlas (SAPIA). *Bothalia*, **37**, 215-248.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

Hui, C., Richardson, D.M., Robertson, M.P., Wilson, J.R.U. & Yates, C.J. (2011) Macroecology meets invasion ecology: Linking the native distributions of Australian *Acacia* species to invasiveness. *Diversity and Distributions*, **17**, 872-883.

Hulme, P.E. (2012) Weed risk assessment: A way forward or a waste of time? *Journal of Applied Ecology*, **49**, 10-19.

Kaplan, H., van Niekerk, A., Le Roux, J. J., Richardson, D. M. & Wilson, J. R. U. (2014) Incorporating risk mapping at multiple spatial scales into eradication management plans. *Biological Invasions*, **16**, 691-703.

Kaplan, H., van Zyl, H.W.F., Le Roux, J.J., Richardson, D.M. & Wilson, J.R.U. (2012) Distribution and management of *Acacia* implexa (Benth.) in South Africa: A suitable target for eradication? *South African Journal of Botany*, **83**, 23-35.

Kotzé, I., Beukes, H., van den Berg, E. & Newby, T. (2010) National invasive alien plant survey. *Report Number: GW/A/2010/21, Agricultural Research Council, Pretoria*, South Africa.

Křivánek, M., Pyšek, P. & Jarošík, V. (2006) Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. *Conservation Biology*, **20**, 1487-1498.

Kull, C.A. & Rangan, H. (2008) *Acacia* exchanges: wattles, thorn trees, and the study of plant movements. *Geoforum*, **39**, 1258-1272.

Kull, C.A., Shackleton, C.M., Cunningham, P.J., Ducatillon, C., Dufour-Dror, J.-M., Esler, K.J., Friday, J.B., Gouveia, A.C., Griffin, A.R., Marchante, E., Midgley, S.J., Pauchard, A., Rangan, H., Richardson, D.M., Rinaudo, T., Tassin, J., Urgenson, L.S., von Maltitz, G.P., Zenni, R.D. & Zylstra, M.J. (2011) Adoption, use and perception of Australian *Acacia* species around the world. *Diversity and Distributions*, **17**, 822-836.

Kull, C.A. & Tassin, J. (2012) Australian *Acacia* species: useful and (sometimes) weedy. *Biological Invasions*, **14**, 2229-2233.

Lake, J.C. & Leishman, M.R. (2004) Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation*, **117**, 215-226.

Le Maitre, D.C., Gaertner, M., Marchante, E., Ens, E.J., Holmes, P.M., Pauchard, A., O'Farrell, P.J., Rogers, A.M., Blanchard, R., Blignaut, J. & Richardson, D.M. (2011) Impacts of invasive Australian *Acacia* species: Implications for management and restoration. *Diversity and Distributions*, **17**, 1015-1029.

Le Maitre, D.C., van Wilgen, B., Gelderblom, C., Bailey, C., Chapman, R. & Nel, J. (2002) Invasive alien trees and water resources in South Africa: case studies of the costs and benefits of management. *Forest Ecology and Management*, **160**, 143-159.

Le Maitre, D.C., Versfeld, DB, & Chapman, R.A. (2000) The impact of invading alien plants on surface water resources in South Africa: Prelimiary assessment. *WaterSA*, **26**, 397-408.

Le Roux, J.J., Brown, G.K., Byrne, M., Ndlovu, J., Richardson, D.M., Thompson, G.D. & Wilson, J.R.U. (2011) Phylogeographic consequences of different introduction histories of invasive Australian *Acacia* species and Paraserianthes lophantha (Fabaceae) in South Africa. *Diversity and Distributions*, **17**, 861-871.

Levine, J.M., Vila, M., Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 775-781.

Lockwood, J.L., Cassey, P. & Blackburn, T.M. (2009) The more you introduce the more you get: The role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions*, **15**, 904-910.

Loiselle, B.A., Howell, C.A., Graham, C.H., Goerck, J.M., Brooks, T. & Smith, K.G. & Williams, P.H. (2003) Avoiding pitfallsof using species distribution models in conseration planning. *Conservation Biology*, **17**, 1591-1600.

Mack, R.N. (2005) Assessing Biotic Invasions in Time and Space: The Second Imperative. *Invasive Alien Species: A New Synthesis* (ed. by R.N.M. Harold M. Mooney, Jeffrey A. Mcneely, Laurie E Neville, Peter Johan Schei, and Jeffrey K. Waage). Island Press, Washington D.C., USA.

Marchante, H., Freitas, H., & Hoffmann, J.H. (2011) Assessing the suitability and safety of a well-known bud-galling wasp, *Trichilogaster Acaciaelongifoliae* for biological control of *Acacia longifolia* in Portugal. *Biological Control*, **56**,193-201.

Martinez-Meyer, E., Townsend Peterson, A. & Hargrove, W.W. (2004). Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecolgy and Biogeography*, **13**, 305–314.

McGeoch, M.A., Butchart, S.H.M., Spear, D., Marais, E., Kleyhans, E.J., Symes, A., Chanson, J. & Hoffmann J (2010) Global indicator of biological invasion: species numbers, biodiversity impact and policy responses. *Diversity and Distributions* , **16**, 95-108.

McGeoch, M.A., Spear, D., Kleynhans, E.J. & Marais, E. (2012) Uncertainty in invasive alien species listing. *Ecological Applications*, **22**, 959-971.

McGregor, K.F., Watt, M.S., Hulme, P.E. & Duncan, R.P. (2012a) What determines pine naturalization: species traits, climate suitability or forestry use? *Diversity and Distributions*, **18**, 1013-1023.

McGregor, K.F., Watt, M.S., Hulme, P.E. & Duncan, R.P. (2012b) How robust is the Australian Weed Risk Assessment protocol? A test using pine invasions in the Northern and Southern hemispheres. *Biological Invasions*, **14**, 987-998.

McNeely, J.A., H.A.M., Neville, L.E., Schei, P.J., &Waage, J.K. (2005) A Global Strategy on Invasive Alien Species: Synthesis and Ten Strategic Elements. *Invasive Alien Species: A New Synthesis* (ed. by R.N.M. Harold M. Mooney, Jeffrey A. Mcneely, Laurie E Neville, Peter Johan Schei, and Jeffrey K. Waage). Island Press, Washington D.C., USA.

Meyerson, L.A. & Mooney, H.A. (2007) Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment*, **5**, 199-208.

Mgidi, T.N., Le Maitre, D.C., Schonegevel, L., Nel, J.L., Rouget, M. & Richardson, D.M. (2007) Alien plant invasions-incorporating emerging invaders in regional prioritization: A pragmatic approach for Southern Africa. *Journal of Environmental Management*, **84**, 173-187.

Miller, J.T., Murphy, D.J., Brown, G.K., Richardson, D.M. & González-Orozco, C.E. (2011) The evolution and phylogenetic placement of invasive Australian *Acacia* species. *Diversity and Distributions*, **17**, 848-860.

Moore, J.L., Runge, M.C., Webber, B.L. & Wilson, J.R. (2011) Contain or eradicate? Optimizing the management goal for Australian *Acacia* invasions in the face of uncertainty. *Diversity and Distributions*, **17**, 1047-1059.

Morris, J. & Glen, H. (1978) PRECIS, the National Herbarium of South Africa (PRE) computerized information system. *Taxon*, **27**, 449-462.

Morris, T.L., Esler, K.J., Barger, N.N., Jacobs, S.M. & Cramer, M.D. (2011) Ecophysiological traits associated with the competitive ability of invasive Australian *Acacia* species. *Diversity and Distributions*, **17**, 898-910.

Mucina, L. & Rutherford, M.C. (2006) Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria, 807pp.

Nel, J.L., Richardson, D.M., Rouget, M., Mgidi, T.N., Mdzeke, N., Le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L. & Neser, S. (2004) A proposed classification of invasive alien plant species in South Africa: Towards prioritizing species and areas for management action. *South African Journal of Science*, **100**, 53-64.

Nix, H.A. (1986) A biogeographic analysis of Australian elapid snakes. *Atlas of Elapid Snakes of Australia*(ed. by R. Longmore), Australian Government Publications Service, Cranberra. 4-15 pp.

Nuñez, M.A. & Medley, K.A. (2011) Pine invasions: Climate predicts invasion success; something else predicts failure. *Diversity and Distributions*, **17**, 703-713.

Orchards, A.E. & Wilson, A. J.G. (eds). (2001) Flora of Australia, Volume 11A & 11B. New South Wales: CSIRO publishing/ABRS.

Pauchard, A., Cavieres, L.A. & Bustamante, R.O. (2004) Comparing alien plant invasions among regions with similar climates: Where to from here? *Diversity and Distributions*, **10**, 371-375.

Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology*, **78**, 419-433.

Peterson, A.T. (2011) Ecological niche conservatism: A time-structured review of evidence. *Journal of Biogeography*, **38**, 817-827.

Peterson, A.T. & Holt, R.D. (2003) Niche differentiation in Mexican birds: Using point occurrences to detect ecological innovation. *Ecology Letters*, **6**, 774-782.

Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265-1267.

Pheloung, P.C., Williams, P.A. & Halloy, S.R. (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management*, **57**, 239-251.

Poynton, R.J. (1979a) *Tree Planting in Southern Africa. The Pines*. Department of Forestry Pretoria, South Africa, 576 pp.

Poynton, R.J. (1979b) *Tree Planting in Southern Africa. The Eucalypts*. Department of Forestry Pretoria. South Africa, 882 pp.

Poynton, R.J. (2009) *Tree Planting in Southern Africa: Other Genera*. Deapartment of Forestry Pretoria, South Africa, 773pp.

Pyšek, P., Jarošík, V. & Pergl, J. (2011) Alien plants introduced by different pathways differ in invasion success: Unintentional introductions as a threat to natural areas. *PLoS ONE*, **6**, 1-11.

Pyšek, P., Křivánek, M. & Jarošik, V. (2009) Planting intensity, residence time, and species traits determine invasion success of alien woody species. *Ecology*, **90**, 2734-2744.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M. & Kirschner, J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131-143.

Reichard, S.H. & Hamilton, C.W. (1997) Predicting invasions of woody plants introduced into North America. *Prediccion de invasiones de plantas lenosas introducidas a Norteamerica*, **11**, 193-203.

Rejmánek, M. & Pitcairn, M. (2002) When is eradication of exotic pest plants a realistic goal. *Turning the tide: the eradication of invasive species* (ed. by C. R. Veitch and M. N. Clout) Invasive Species Specialist Group, IUCN [World Conservation Union], Gland Switzerland, and Cambridge, UK.

Rejmánek, M. & Richardson, D.M. (2013) Trees and shrubs as invasive alien species - 2013 update of the global database. *Diversity and Distributions*, **19**, 1093-1094.

Rejmánek, M., Richardson, D.M., Pyšek, P. (2005). Plant invasions and invasibility of plant communities *Vegetation ecology* (ed. by van der Maarel, E.) oxford, Blackwell.

Rich, T. & Woodruff, E. (1992) Recording bias in botanical surveys. *Watsonia*, **19**, 73-95.

Richardson, D.M. (1998) Forestry trees as invasive aliens. *Conservation Biology*, **12**, 18-26.

Richardson, D.M., Carruthers, J., Hui, C., Impson, F.A.C., Miller, J.T., Robertson, M.P., Rouget, M., Le Roux, J.J. & Wilson, J.R.U. (2011) Human-mediated introductions of Australian *Acacia* species - a global experiment in biogeography. *Diversity and Distributions*, **17**, 771-787.

Richardson, D.M. & Kluge, R.L. (2008) Seed banks of invasive Australian *Acacia* species in South Africa: Role in invasiveness and options for management. *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 161-177.

Richardson, D.M. & Pyšek, P. (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytologist*, **196,** 383-396.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Dane Panetta, F. & West, C.J. (2000) Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions*, **6**, 93-107.

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

Robertson, M.P., Villet, M.H. & Palmer, A.R. (2004) A fuzzy classification technique for predicting species' distributions: applications using invasive alien plants and indigenous insects. *Diversity and Distributions*, **10**, 461-474

Rodríguez-Echeverría, S., Fajardo, S., Ruiz-Díez, B. & Fernández-Pascual, M. (2012) Differential effectiveness of novel and old legume–rhizobia mutualisms: implications for invasion by exotic legumes. *Oecologia*, **170**, 253-261.

Rodríguez-Echeverría, S., Le Roux, J.J., Crisóstomo, J.A. & Ndlovu, J. (2011) Jack-of-all-trades and master of many? How does associated rhizobial diversity influence the colonization success of Australian *Acacia* species? *Diversity and Distributions*, **17**, 946-957.

Rouget, M., Richardson, D.M., Nel, J.L., Le Maitre, D.C., Egoh, B. & Mgidi, T. (2004) Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climatic suitability. *Diversity and Distributions*, **10**, 475-484.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. (2001) The Population Biology of Invasive Specie. *Annual Review of Ecology and Systematics*, **32**, 305-332.

Scott, J.K. & Panetta, F.D. (1993) Predicting the Australian weed status of southern African plants. *Journal of Biogeography*, **20**, 87-93.

Seabloom, E.W., Williams, J.W., Slayback, D., Stoms, D.M., Viers, J.H. & Dobson, A.P. (2006) Human impacts, plant invasion, and imperiled plant species in California. *Ecological Applications*, **16**, 1338-1350.

Shackleton, S., Kirby, D. & Gambiza, J. (2011) Invasive plants - friends or foes? contribution of prickly pear (Opuntia ficus-indica) to livelihoods in Makana Municipality, Eastern Cape, South Africa. *Development Southern Africa*, **28**, 177-193.

Shaughnessy, G.L. (1980) *Historical ecology of alien woody plants in the vicinity of Cape Town, South Africa*. School of Environmental Studies, University of Cape Town.

Simberloff, D. & Gibbons, L. (2004) Now you see them, now you don't - population crashes of established introduced species. *Biological Invasions* **6**, 161-172

Soberón, J., Peterson A.T (2005) Interpretation of Models of Fundamental Ecological Niches and Species Distributional Areas. *Biodiversity Informatics*, **2**, 1-10.

Steiner, F.M., Schlick-Steiner, B.C., VanDerWal, J., Reuther, K.D., Christian, E., Stauffer, C., Suarez, A.V., Williams, S.E. & Crozier, R.H. (2008) Combined modelling of distribution and niche in invasion biology: A case study of two invasive Tetramorium ant species. *Diversity and Distributions*, **14**, 538-545.

Stoett, P. (2010) Framing bioinvasion: biodiversity, climate change, security, trade, and global governance. *Global Governance: A Review of Multilateralism and International Organizations*, **16**, 103-120.

Thompson, G.D., Robertson, M.P., Webber, B.L., Richardson, D.M., Le Roux, J.J. & Wilson, J.R.U. (2011) Predicting the subspecific identity of invasive species using distribution models: *Acacia saligna* as an example. *Diversity and Distributions*, **17**, 1001-1014.

Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O. & Rouget, M. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, **11**, 2234-2250.

Thuiller, W., Richardson, D.M., Rouget, M., Procheş, Ş. & Wilson, J.R.U. (2006) Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology*, **87**, 1755-1769.

Van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J.M. & Fischer, M. (2010) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters*, **13**, 947-958.

Van Wilgen, B.W., De Wit, M., Anderson, H., Le Maitre, D., Kotze, I., Ndala, S., Brown, B. & Rapholo, M. (2004) Costs and benefits of biological control of invasive alien plants: case studies from South Africa. *South African Journal of Botany*, **100**, 113-123.

Van Wilgen, B.W., Dyer, C., Hoffmann, J.H., Ivey, P., Le Maitre, D.C., Moore, J.L., Richardson, D.M., Rouget, M., Wannenburgh, A. & Wilson, J.R.U. (2011) National-scale strategic approaches for managing introduced plants: Insights from Australian *Acacia* species in South Africa. *Diversity and Distributions*, **17**, 1060-1075.

Williamson, M. (2006) Explaining and predicting the success of invading species at different stages of invasion. *Biological Invasions*, **8**, 1561-1568.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661-1666.

Willis, J.H. (1970) *A handbook to plants in Victoria*. Melbourne University Press Melbourne.

Wilson, J.R.U., Caplat, P., Dickie, I.A., Hui, C., Maxwell, B.D., Nuñez, M.A., Pauchard, A., Rejmánek, M., Richardson, D.M., Robertson, M.P., Spear, D., Webber, B.L., van Wilgen, B.W. & Zenni, R.D. (2014) A standardized set of metrics to assess and monitor tree invasions. *Biological Invasions*, **16**, 535-551

Wilson, J.R.U., Gairifo, C., Gibson, M.R., Arianoutsou, M., Bakar, B.B., Baret, S., Celesti-Grapow, L., Ditomaso, J.M., Dufour-Dror, J.M., Kueffer, C., Kull, C.A., Hoffmann, J.H., Impson, F.A.C., Loope, L.L., Marchante, E., Marchante, H., Moore, J.L., Murphy, D.J., Tassin, J., Witt, A., Zenni, R.D. & Richardson, D.M. (2011) Risk assessment, eradication, and biological control: Global efforts to limit Australian *Acacia* invasions. *Diversity and Distributions*, **17**, 1030-1046.

Wilson, J.R.U, Ivey, P., Manyama, P., & Nänni, I. (2013) A new national unit for invasive species detection, assessment and eradication planning. *South African Journal of Science*, **109**, 1-13.

Wilson, J.R.U., Richardson, D.M., Rouget, M., Procheş, Ş., Amis, M.A., Henderson, L. & Thuiller, W. (2007) Residence time and potential range: Crucial considerations in modelling plant invasions. *Diversity and Distributions*, **13**, 11-22.

Wittenberg, R. & Cock, M.J. (2005) *Invasive alien species: a toolkit of best prevention and management practices*. ed. by R.N.M. Harold M. Mooney, Jeffrey A. Mcneely, Laurie E Neville, Peter Johan Schei, and Jeffrey K. Waage). Island Press, Washington D.C., USA.

Zenni, R.D. & Nuñez, M.A. (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. *Oikos*, **122**, 801-815.

Zenni, R.D., Wilson, J.R.U., Le Roux, J.J. & Richardson, D.M. (2009) Evaluating the invasiveness of *Acacia paradoxa* in South Africa. *South African Journal of Botany*, **75**, 485-496.

Zhu, L., Sun, O.J., Sang, W., Li, Z. & Ma, K. (2007) Predicting the spatial distribution of an invasive plant species (Eupatorium adenophorum) in China. *Landscape Ecology*, **22**, 1143-1154.

6 Appendices

6.1 Appendix I: Potential distributions of sixteen species that are not widespread in southern Africa arranged alphabetically.

Acacia acuminata

A. adunca

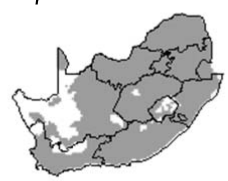
A. aneura

A. binervata

A. cultriformis

A. falciformis

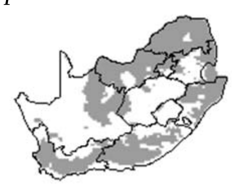
A. fimbriata



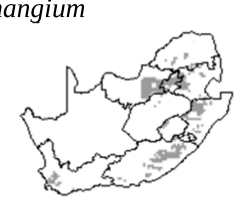
A. implexa

A. mangium

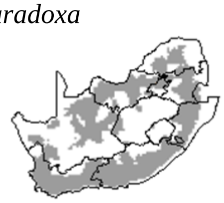
A. paradoxa



A. pendula



A. prominens



A. retinodes

A. rubida

A. stricta

A. schinoides

A. viscidula

6.2 Appendix II: A categorisation scheme for populations in the unified framework (Source: Blackburn *et al*., 2011)

Category	Definition
A	Not transported beyond limits of native range
B1	Individuals transported beyond limits of the native range, and in captivity or quarantine (i.e. individuals provided with conditions suitable for them, but explicit measures of containment are in place
B2	Individuals transported beyond limits of native range, and in cultivation (i.e. individuals provided with conditions suitable for them, but explicit measures to prevent dispersal are limited at best
B3	Individuals transported beyond limits of the native range, and directly released into novel environment
C0	Individuals released into the wild (i.e. outside of captivity or cultivation) in location here introduced, but incapable of surviving for a significant period
C1	Individuals surviving in the wild (i.e. outside of captivity or cultivation) in location where introduced, no reproduction
C2	Individuals surviving in the wild in location where introduced reproduction occurring, but not self-sustaining
C3	Individuals surviving in the wild in location here introduced reproduction occurring, and self-sustaining
D1	Self-sustaining population in the wild, with individuals surviving a significant distance from the original point of introduction
D2	Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction
E	Fully invasive species, with individual dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence