The invasion ecology of *Acacia elata* (A. Cunn. Ex Benth.) with implications for the management of ornamental wattles

by
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Thesis presented in fulfilment of the requirements for the degree of Masters in the Faculty of Science at Stellenbosch University

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Co-supervisor: Dr. John R. Wilson

December 2013

Declaration

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

September 2013

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Abstract

This thesis explores how human dictated methods of introduction and species-specific traits interact to define spatial patterns in invasive plant populations using *Acacia elata* as a model species. I initially asked whether the relatively small invasive extent (when compared to congeners introduced for forestry or dune stabilization) of a species used widely for ornamental purposes (*A. elata*) is due to low rates of reproduction in South Africa. Results indicate that *A. elata* has similar traits to other invasive Australia *Acacia* species: annual seed input into the leaf litter was high (up to 5000 seeds m^{-2}); large seedbanks develop (>20 000 seeds m^{-2}) in established stands; seed germinability is very high (>90%); seeds accumulate mostly in the top soil layers but can infiltrate to depths of 40cm; and seed germination appears to be stimulated by fire. I argue that the current limited distribution of invasive *A. elata* populations is not attributable to species-specific reproductive traits. Following on from this I addressed the relative importance of species traits, the recipient environment, and introduction dynamics using species distribution models and spread models defined using a range of parameters representative of invasive Australian acacia species. Results indicate that in the early stages of simulated invasions, the number of trees introduced was the most important parameter influencing abundance and extent, while the placement of introduction foci in urban areas associated with ornamental introductions limited the extent and abundance of invasive populations. I suggest that conditions relating to human-mediated introduction events initially mask the influence of intrinsic species traits and help to explain the failure and success of species associated with specific human-shaped pathways. Third, I used scale-area curves to determine how these human-dictated introduction conditions influenced the spatial structure of populations. The fractal

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dimension (D_{ij}) of *A. elata* populations indicates plot scale (2.5-25m) spread with high densities that are increasing. Artefacts of introduction history were observed at the regional scale (2.5-25km) - populations are contiguous around introduction foci such as towns and roads. Moreover, fragmentation of *A. elata* populations at local to landscape scales (0.25-2.5km) is due to a combination of the haphazard regional placement and limited secondary dispersal vectors, both of which can be linked to their introduction history. In summary, this study used a combination of field-based data, modelling techniques and broad-scale sampling methods to assess how intrinsic species traits and introduction conditions mediate invasive spread. I conclude that introduction history can have a long-lasting (100+ years) influence on the spatial structure and distribution of invasive plants, which can mask the influence of individual species traits.

Opsomming

Alhoewel menigte plant spesies deur mense ingevoer word, word slegs 'n klein hoeveelheid van plante indringers. Die beperkte aantal spesies wat in nuwe habitatte vestig en versprei, kan grotendeels toegeskryf word aan die omgewing en mensgemaakte hindernisse ten opsigte van oorlewing, voortplanting en verspreiding. In hierdie tesis gebruik ek *Acacia elata* as 'n model spesie om te ondersoek hoe die invoeringsproses sowel as spesie spesifieke eienskappe die ruimtelike struktuur van indringende populasies bepaal. Aanvanklik was my vraag of die relatiewe klein indringingsarea van 'n spesie wat ingevoer is vir ornamentele doeleindes (*Acacia elata*), teenoor die groot indringingsareas van Australiese *Acacia*-spesies wat ingevoer is vir bosbou of duin stabilisering, die gevolg is van lae voortplantings tempo in Suid-Afrika. Resultate dui daarop dat *A. elata* soortgelyke eienskappe as ander indringende Australië akasia spesies het: jaarlikse saad produksie is hoog (tot 5000 sade m^{-2}); groot ontwikkelde saadbanke (> 20 000 sade m^{-2}); hoë saad ontkieming (> 90 %); saad versamel in die boonste grondlae, alhoewel dit kan infiltreer tot 'n diepte van 40 cm; laastens, ontkieming word deur vuur gestimuleer. Hierdie resultate stel voor dat die huidige beperkte verspreiding van indringende *A. elata* populasies nie die gevolg is van spesie spesifieke voortplantings eienskappe nie. Gevolglik het ek 11 indringende Australiese akasia-spesies ondersoek om die relatiewe belangrikheid van spesie eienskappe, die area waar hul geplant is, asook invoerings aspekte te ondersoek. Resultate wys dat die aantal bome wat ingevoer is, die belangrikste eienskap was ten opsigte van digtheid en verspreiding van 'n indringende spesie, terwyl invoering naby fokuspunte in stedelike gebiede weer spesie digtheid en verspreiding beperk. Hierdie resultate toon dat spesies eienskappe aanvanklik nie 'n groot invloed het op hul sukses nie, maar dat hul sukses eerder afhang van waar hul geplant word.

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Derdens, gebruik ek skaal - area kurwes om te bepaal hoe die invoering van *A. elata* die ruimtelike struktuur van populasies beïnvloed het. Die fraktale dimensie (Dij) van *A. elata* bevolkings dui op verspreiding by die plaaslike vlak (2,5 - 25m), wat voorstel dat verspreiding nie op hierdie skaal beperk is nie. Eienskappe van die rede/metode van invoering was wel waargeneem op die groter skaal (2.5 - 25km) waar populasies digter was naby dorpe en paaie. Die intermediêre skaal (0,25 - 2.5km) dui daarop dat *A. elata* populasies huidiglik beperk word deur 'n kombinasie van lukrake plasing en beperkte sekondêre verspreiding, albei wat gekoppel kan word aan hul invoer geskiedenis. Hierdie studie maak dus gebruik van 'n kombinasie van veld gebaseerde data, modellerings tegnieke en breë skaal steekproefmetodes om te evalueer hoe algemene spesies eienskappe en invoer toestande verspreiding bepaal. Sodoende verskaf ek 'n raamwerk om die invloed van invoer toestande op die ruimtelike struktuur en verspreiding van ornamentele plant indringers te verstaan.

Acknowledgements

First and foremost I thank my supervisors for their substantial contribution in the form of ideas, comments and guidance over the last two years.

I am grateful to all contributing authors on the four respective papers appearing in this thesis for their advice and encouragement, as well as Matthys Strydom, Vernon Visser and Ruan Veldtman for suggestions regarding methodology.

I thank Anél Garthwaite and Christy Momberg for their excellent administrative assistance.

Special thanks to the few friends who I have left and my family and girlfriend who have been forced to support me along the way.

I am sincerely thankful to all the landowners who gave me permission to abuse their non-native flora and Cape Nature for providing permits to work within the Western Cape.

Finally, I acknowledge financial support from the Drakenstein Trust through the DST-NRF Centre of Excellence for Invasion Biology.

For further details see the acknowledgements section in chapters three and four.

Contents

Preface

The three data chapters in this thesis were written for and submitted to journals as they were completed. Therefore each chapter is presented in the format of a journal article. To maintain consistency, all referencing and formatting follows that of the journal *Global Change Biology*. During this work I interacted with a number of scientists whose collaboration has been extremely beneficial to me in furthering my understanding of both plant invasions and broader aspects of ecology. Collaboration with other authors has greatly improved the quality of papers submitted to journals and for this thesis. I have thus outlined the contribution of authors to relevant chapters.

Chapter 2-This chapter is based on: Donaldson JE, Richardson DM, Wilson JRU. Unpublished. The seed ecology of an ornamental wattle in South Africa—the growing invasive problem of *Acacia elata* (A. Cunn. Ex Benth.). Submitted: *South African Journal of Botany*.

Author contributions: JED designed the framework with refinements from DMR and JRUW. JED carried out field work, data collection and statistical analysis. JRUW advised on statistical methods. JED wrote the paper with DMR and JRUW providing comments and refining writing.

Chapter 3-This chapter is based on: Donaldson JE, Hui C, Richardson DM, Webber BL, Robertson MP, Wilson JRU. Unpublished. Invasion trajectory of alien trees: the role of introduction pathway and planting history. In Revision: *Global Change Biology*.

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Author contributions: JED designed the framework with refinements from CH, DMR, MPR, BLW and JRUW. JED collated distribution records and cleaned the data with help from BLW. JED designed and ran species distribution models with advice from MPR and BLW. JED and CH designed the spread model with CH providing support with coding. JED performed statistical analysis with advice from JRUW. JED wrote the paper with all other authors aiding in refinement and improvement of structure and wording.

Chapter 4-This chapter is based on: Donaldson JE, Richardson DM, Wilson JRU. Unpublished. Scale area curves reveal importance of planting history in shaping the national-scale distribution of an invasive tree. Accepted: *Biological Invasions*.

Author contributions: JED designed the framework with refinements from DMR and JRUW. JED carried out field work, data collection and statistical analysis. JRUW advised on statistical methods. JED wrote the paper with DMR and JRUW providing comments and refining writing.

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Chapter 1: Introduction

Humans have been significantly manipulating the distribution of plant species for at least the past 500 years. Human-mediated movement of plants was initially associated with the need for resource security in newly colonized areas (Mack, 2003). However, over the past century the rise of global trade and long-distance transportation has resulted in a continuous increase in the reasons driving human-mediated dispersal (Reichard & White, 2001; Mack, 2003). The result is a spike in both the number of species introduced to new ranges and the number of seeds, seedlings, and plants deliberately introduced globally. A small proportion of these introduced species become established and invasive in their new landscapes. The economic costs of these biological invasions often outweigh the benefits associated with their introduction (Pimentel *et al*., 2000, 2005). Determining both factors that promote these invasions and those that limit them is valuable for organizations looking to limit the overall negative impacts of often-necessary global species movements.

1.1 Deliberate introductions and the Introduction-naturalization-invasion continuum

For a species to successfully establish and spread in regions outside their novel range it needs to overcome a number of barriers (Blackburn *et al.,* 2011; **Fig. 1.1**). The first barrier to the establishment of any species in a novel environment is the geographical barrier related to the transport of a species to the new area (Wilson *et al*., 2009; Blackburn *et al*., 2011). In the case of deliberate human-mediated dispersal this barrier is negated by human-aided transport of seeds and plants to new areas. Ultimately, the major barriers facing a species introduced for deliberate human use are those related to reproduction, dispersal and the

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recipient environment (Blackburn *et al.*, 2011). The size of the introduced population, its placement in the landscape, the positioning of introduction foci, species traits and recipient environment have all been shown to play important roles in the capacity for populations or species to overcome these barriers (Lonsdale, 1999; Lockwood *et al.,* 2005; Thuiller *et al.,* 2006). In the case of deliberate introductions all of these aspects will be determined and shaped to some degree by the reason a species is being introduced. Species with similar human uses will have similar introduction pathways; that is, they should have certain commonalities in the conditions associated with their introduction and dissemination (Wilson *et al.,* 2007; Blackburn *et al.,* 2011). Such commonalities should result in distinctive biogeographical patterns in the invasive ranges – a "signature" that may remain discernible for long periods (decades or centuries; Castro-Díez *et al.*, 2011).

1.2 Invasive Australian acacia in South Africa: a model study group

At least 80 Australian *Acacia* species were introduced to and disseminated throughout South Africa over the last 150 years (Poynton, 2009; Le Roux *et al*., 2011; Richardson *et al*., 2011a). Throughout the thesis, use of the vernacular "acacia" refers to the group of 1012 recognised *Acacia* species, previously grouped in *Acacia* subgenus *Phyllodineae*, which are native to Australia (Richardson *et al*. 2011a). Acacia introductions to South Africa initially focused on utilitarian requirements such as forestry and dune stabilization (See Avis, 1989; Poynton, 2009 for reviews). However, a number of species were widely disseminated as ornamental plants (Poynton, 2009). Fourteen acacias are currently invasive in South Africa (Van Wilgen *et al*., 2011). Aside from the current costs of managing these invasive species, the presence of currently non-invasive species in the country and the fact that even the most widespread invasive species have not yet invaded all potentially suitable habitat in the

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country (Rouget *et al.*, 2004) represents a significant "invasion debt" (expenses related to control of future invasions stemming from current and future introduction events sensu Essl *et al.*, 2010), making this group of plants a huge economic burden for the country, now and into the future. Due to the realized threat of these species, much research and management has focused on these species, and substantial data exist for the major invaders (Milton & Hall, 1981; Henderson, 2006; Richardson & Kluge, 2008; Marchante *et al.*, 2010; Gibson *et al.*, 2011; Strydom *et al.*, 2011). The many reasons for introduction and dissemination of these species, the availability of data on invasive traits, distributions and introduction histories, and variation in current occupancy of potential distributions make acacia invasions in South Africa an excellent model group for investigating trends and patterns in invasion ecology (Richardson *et al.*, 2011a; Kueffer *et al.*, 2013).

Although the fourteen invasive *Acacia* species have been present in South Africa for similar lengths of time, their extents of invasion differ considerably (Nel *et al.*, 2004; Wilson *et al.*, 2007; Van Wilgen *et al.*, 2011). Commercial forestry species and dune stabilization have much larger invasive ranges and occur in higher abundances in South Africa than those used for ornamentation (**Fig. 1.2**). This aspect of acacia invasions has not yet received much attention and an understanding of why species introduced as ornamentals have not (yet) become invasive to the same extent as ecologically similar commercial forestry species and dune stabilization is required to quantify the overall invasion debt for the group which is a requirement for strategic planning (van Wilgen *et al.*, 2011). Acquiring insights into how human uses have shaped acacia introductions will also provide information on which to base robust strategies for deciding on particular management interventions (Van Wilgen *et al.*, 2011).

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The chapters in my thesis follow the pathway of the introduction-naturalization-invasion continuum (**Fig. 1.1**) to investigate the role of aspects of introductions pathways in determining the capacity of species to spread and invade. Special attention is given to such factors associated with introductions of acacias for ornamentation. Insights gained from this work are then used to develop guidelines for the improved management plan for one species: *Acacia elata*.

1.3 Are ornamental species limited by reproductive traits? (Chapter 2)

For a tree species to escape cultivation, survive and spread it needs to reproduce. There is a substantial amount of literature on the factors that mediate effective reproduction of the major invasive acacia species and the traits that influence invasion success in the group (Milton & Hall, 1981; Richardson & Kluge, 2008; Marchante *et al*., 2010; Gibson *et al*., 2011; Strydom *et al*., 2011). Similar work on acacia species introduced for ornamentation is lacking. It is possible that due to the substantially lower numbers of trees introduced and reduced selection pressures related to the ornamental trade acacia species introduced for ornamentation are not as reproductively successful in South Africa as other more invasive species. Thus in **Chapter 2** of my thesis, I address key aspects of the seed biology of the ornamental tree *Acacia elata* A. Cunn. ex Benth. (**Fig. 1.3**) and compare results with those from previous work on traits associated with the success of other invasive acacia species (reviewed in Richardson & Kluge, 2008; Gibson *et al*., 2011). Specifically, I explore whether the limited extent of invasive populations of *A. elata* in South Africa can be attributed to inherent reproductive limitations.

1.4 Are ornamental species limited by planting history? (Chapter 3)

Studies of species that have successfully established and become invasive and those that have failed have identified factors linked to events and practices associated with introduction history (Lonsdale, 1999; Lockwood *et al*., 2005, 2009; Thuiller *et al*., 2006; Castro-Díez *et al*., 2011). Consequently, it has been argued that invasion patterns are better explained by factors that shaped their introduction than by invoking intrinsic species traits (Lonsdale, 1999; Lockwood *et al*., 2005; Thuiller *et al*., 2006; Wilson *et al*., 2009; Castro-Díez *et al*., 2011; Proceş *et al*., 2012). Of particular importance is the initial dispersal phase of an invasion which involves the introduction and placement of species in the new habitat and thus is fundamental to the rest of the invasion process (Puth & Post, 2005). Despite the importance of the initial stages of invasion, little work has focused on its effects on invasion dynamics. In **Chapter 3** of my thesis I look at how elements of the reason for introduction have shaped the spread and abundance of invasive acacia species in South Africa to address two hypotheses: 1) Forestry and dune stabilization species will have closer climate matches between alien and native populations than ornamental species; 2) introduction type and human-aided dispersal are more important than species traits in determining the invasiveness of alien populations, at least initially. I test these hypotheses using a combination of species distribution models and spread models.

1.5 How important are introduction history and species-specific traits in shaping population structure at different spatial and temporal scales? (Chapter 4)

One important aspect to bear in mind when studying the biogeography of invasive species is that in most cases species have not reached an equilibrium state within the new region (Rouget *et al*., 2004). The spatial structure of invasive populations will thus be determined

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by interactions between their intrinsic species traits, linked to dispersal, and the idiosyncrasies of human-related dissemination; residence time is particularly important in this regard (Wilson *et al.*, 2007). In **Chapter 4** of my thesis I utilize the abundance-occupancy relationship to analyse the spatial structure of invasive *A. elata* populations invasions in South Africa and compare them to those of *A. longifolia* (introduced mainly for use in dune stabilization) assessed by Veldtman *et al.* (2010). I use the understanding of the role of intrinsic species traits developed in **Chapter 2** as well as an understanding of how introduction history influences spread developed in **Chapter 3** to determine whether spatial patterns of invasive populations are still influenced by introduction history even more than a century after introduction. In so doing, I aim to develop a more robust framework for analysing invasive populations using the methods related to the abundance-occupancy relationship (Wilson *et al.*, 2004; Veldtman *et al.*, 2010). In particular, I focus on identifying situations where the method of human introduction is still expected to define population spatial patterns and thus requires different interpretation to natural populations in equilibrium with their environment. Puth & Post (2005) highlight the importance of the introduction phase of invasion on the ability of people to understand and manage biological invasions. They suggest that the majority of work to date has focused on the later stages and therefore that vital information regarding invasive success and failure is often overlooked (Puth & Post, 2005). In **Chapter 4** of my thesis I attempt to highlight the importance of the introduction phase of invasion on the spatial structure of an invasive population and develop a framework in which it is possible to identify the start of new invasions when they are in their infancy and management operations have the greatest chance to succeed (Simberloff, 2003; Panetta *et al.*, 2011).

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1.6 Developing a framework for invasive ornamental trees in South Africa

Van Wilgen *et al.*, (2011) addressed the development of a national-scale approach to the management of introduced invasive species in South Africa based on Australian acacias. My final chapter (**Chapter 5**) is a synthesis of the previous three research chapters and uses the results to provide guidelines for national-scale strategic approach for *A. elata* (and potentially invasive ornamental trees in general) following the suggestions outlined in Van Wilgen *et al.*, (2011).

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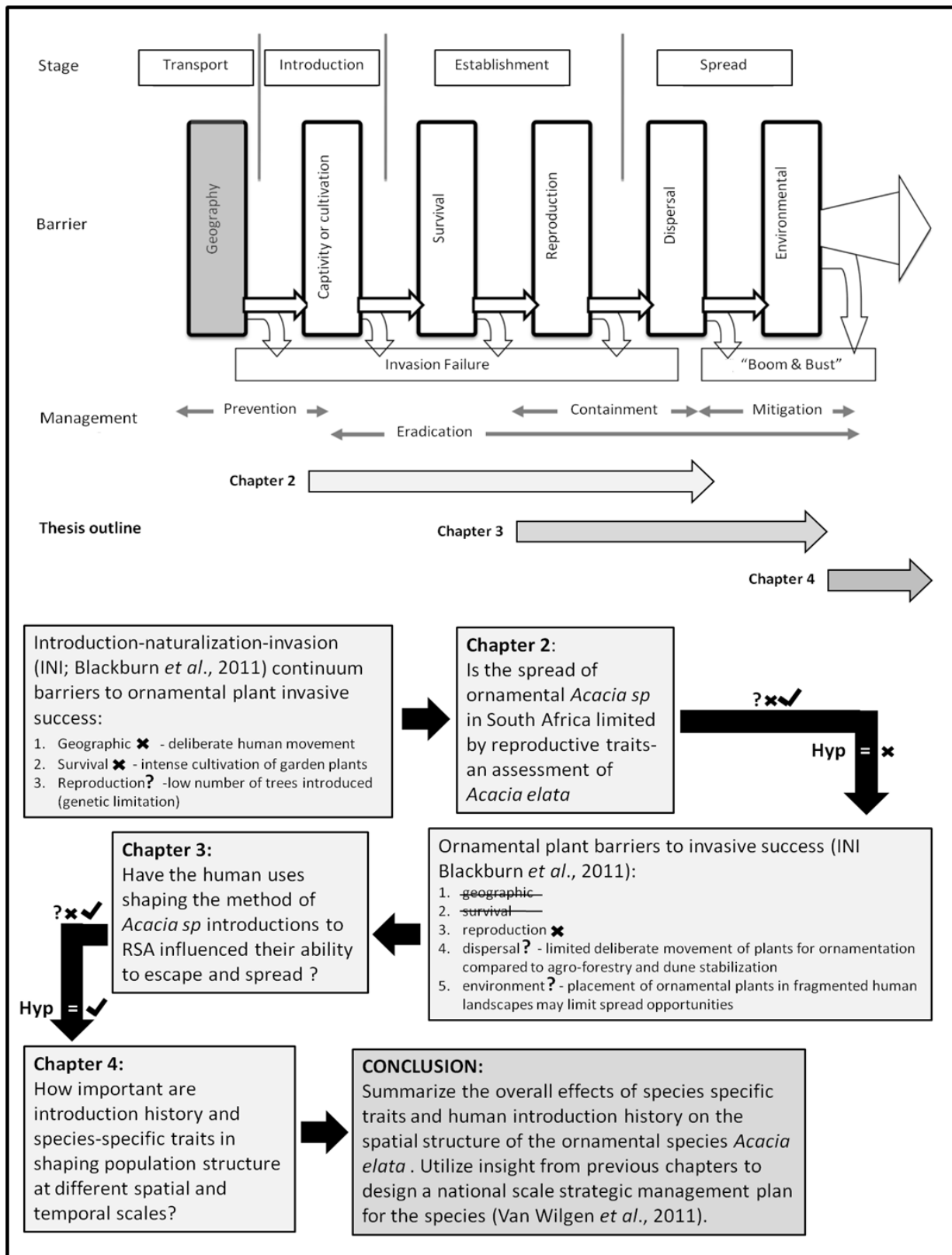
Fig. 1.1 Schematic overview of the aims of each chapter of the thesis-see next page for full caption

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Fig. 1.1 Schematic overview of the aims of each chapter of the thesis with reference to the series of barriers that define the introduction-naturalization-invasion continuum (INIC; Richardson *et al*., 2000b; figure adapted from Blackburn *et al.*, 2011). According to the INIC conceptualization, successive barriers act on species introduced to novel regions and must be overcome for the species to progress to different invasion stages. As ornamental plants are moved deliberately by humans to new areas and often cultivated in novel areas, geographic and survival barriers are generally unimportant in limiting invasions of ornamental plants. Reproduction is thus the first major barrier to invasion. Chapter 2 examines whether aspects of reproductive ecology limit regeneration and spread of *Acacia elata* in South Africa. Chapters 3 and 4 explore different questions and apply different methods to examine the role of factors associated with initial plantings and dissemination in shaping invasion trajectories. In Chapter 3 focus is placed on the influence that introducing plants in fragmented urban environments, differences in propagule pressure, and secondary human dispersal have on the spread of a population compared to intrinsic species traits. Chapter 4 quantifies the impact of processes identified in Chapter 2 and 3 on the spatial structure of *A. elata* populations in South Africa. The concluding chapter summarizes key facets of the invasion ecology with reference to the phases and stages of the INIC and provides guidelines for management.
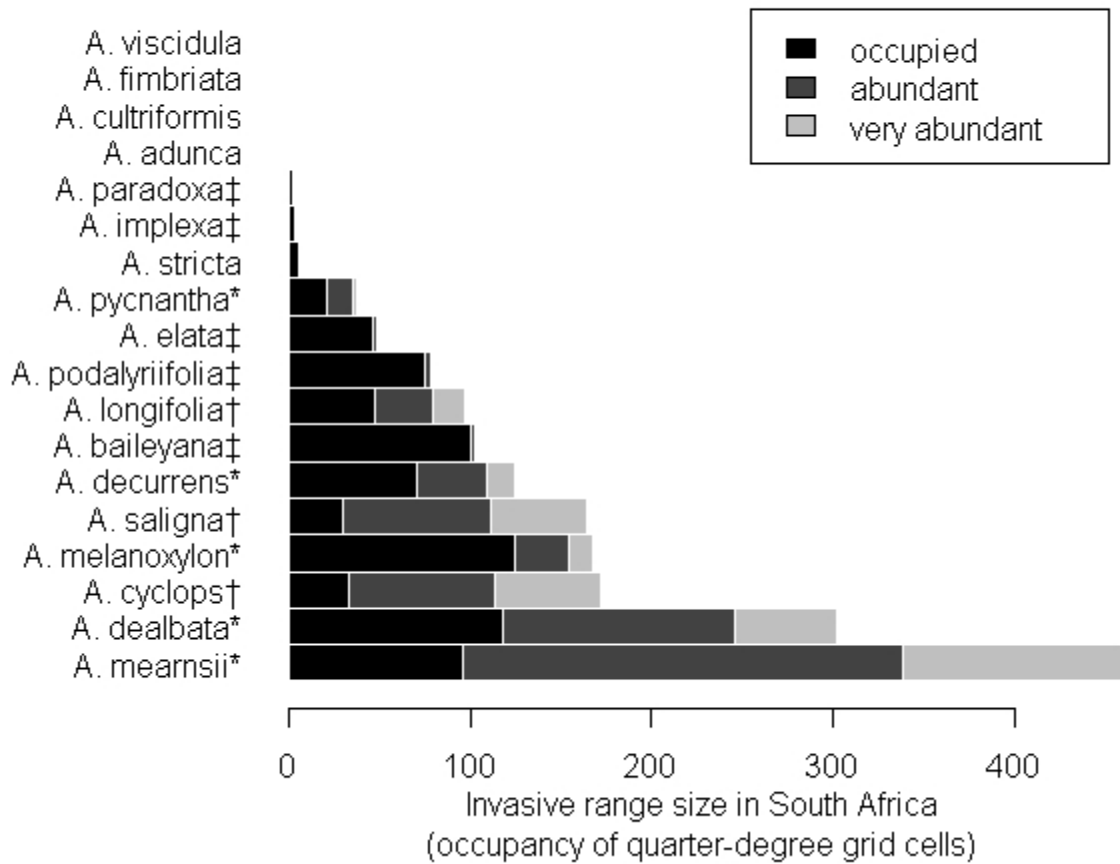
Fig. 1.2 Invasive Australian *Acacia* species introduced to South Africa and disseminated for use in forestry* and dune stabilization† tend to have the largest invasive distributions and be present at the highest densities when compared to species introduced and disseminated as ornaments‡ (Species reason for introduction and dissemination taken from Wilson *et al.*, 2007, those without symbols were only introduced to a small number of localities for forestry trials).

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Fig. 1.3 *Acacia elata* in South Africa. Clockwise from top: (a) planted trees on farm in Elgin; (b) planted tree in suburban Cape town; (c) trees planted in a greenbelt, suburban Cape Town; (d) seedlings growing in an open field near planted garden trees; (e) seedlings growing in neglected land where a planted tree has been felled in Somerset West; (f) seedlings growing under in a pine plantation near Elgin; (g) dense invasive stand on abandoned land near Storms River; (h) invasive stands growing and flowering amongst pine plantations in Somerset West; (i) flowers and pods of adult trees in Somerset West; (j) invasive stand 6 years after mechanical clearing on vacant land near Storms River.

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Chapter 2: The seed ecology of an ornamental wattle in South Africa—the growing invasive problem of *Acacia elata* (A. Cunn. Ex Benth.)

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Keywords: Biological invasions, Fabaceae, reproductive biology, seedbank, tree invasions

Short Communication

Abstract

Australian *Acacia* species introduced as ornamentals have notably smaller invasive ranges in South Africa than those introduced for commercial forestry or dune stabilization. We asked whether the relatively small invasive extent of a species used widely for ornamental purposes (*Acacia elata*) is due to low rates of reproduction in the region. The time to reproductive maturity, seed dispersal, annual seed production, seedbank dynamics and seed germination and viability were assessed at five sites in the Western Cape. Results indicate that *A. elata* has similar traits to other invasive Australia *Acacia* species: annual seed input into the leaf litter was high (up to 5000 seeds m^{-2}); large seedbanks develop (>20 000 seeds m^{-2}) in established stands; seed germinability is very high (>90%); seeds accumulate mostly in the top soil layers but can infiltrate to depths of 40cm; and seed germination appears to be stimulated by fire. However the age at the onset of reproduction is longer than most widespread invaders (~4 years) and dispersal is fairly limited (seeds fell up to distances of 6m from the parent canopy; the highest density of seed rain was found directly under the canopy with over 20% of seeds falling directly under the terminal branches). We argue that the current limited distribution of invasive *A. elata* populations is the result of the relatively small number of plants introduced, the species' apparent lack of secondary dispersal vectors, and the planting of trees in gardens and urban settings where opportunities for recruitment and proliferation are limited. The species is, however, increasing in abundance and range, and is starting to spread into natural vegetation. Management to reduce seed production through classical biological control, as has been achieved for other Australian *Acacia* species in South Africa, should be prioritised.

2.1.　Introduction

Only a small proportion of the very large number of plant species introduced into novel habitats by humans become invasive (Ewel *et al.*, 1999). The limited number of species that establish and spread in novel ranges can largely be attributed to the environmental and manmade barriers to survival, reproduction and dispersal experienced in a new region (Blackburn *et al.*, 2011). Previous studies have shown that that reproductive traits related to seed dispersal, seed production, seed size, and the ability to generate long-lived seedbanks are consistently linked to the likelihood that introduced trees become invasive (Gibson *et al.*, 2011; Gioria *et al.*, 2012). Developing a comprehensive understanding of the seed ecology of introduced species can provide valuable insights into their invasive potential and how they should be managed.

At least 80 Australian *Acacia* species were introduced to and disseminated throughout South Africa over the last 150 years (Poynton, 2009; Le Roux *et al.*, 2011; Richardson *et al.*, 2011). Although the fourteen Australian acacias that are currently invasive in South Africa have been present in South Africa for similar lengths of time, their extents of invasion differ considerably (Nel *et al.*, 2004; Wilson *et al.*, 2007; Van Wilgen *et al.*, 2011). Commercial forestry species and dune stabilization have much larger invasive ranges and occur in higher abundances in South Africa than those used for ornamentation (**Fig. 1.2**). Understanding the reasons for the differences in invasive success is important for developing a robust strategy for managing Australian acacias in South Africa, where some species have yet to colonize large parts of their potential ranges (Rouget *et al.*, 2004). In particular it is important to understand whether those species that were not widely disseminated constitute a

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substantial "invasion debt" (sensu Essl *et al*., 2010) which will require special consideration in strategic planning.

The reproductive ecology of Australian acacias widely used in forestry and dune stabilization in South Africa has been well studied (Milton & Hall, 1981; Richardson & Kluge, 2008; Marchante *et al*., 2010; Gibson *et al.*, 2011; Strydom *et al*., 2011), but such information is lacking for species used primarily for ornamentation. As seed production and dispersal are key elements driving Australian acacia invasions (Richardson & Kluge, 2008), they might explain the differences observed in invasion extent. In this paper we assess key aspects of the seed biology of *Acacia elata* (A. Cunn. Ex Benth.) and compare the outcome to previous work on traits associated with the success of other invasive *Acacia* species (Richardson & Kluge, 2008; Gibson *et al*., 2011). Is the limited extent of invasive populations of *A. elata* in South Africa due to inherent reproductive limitations? The species was selected for this study due to its introduction and dissemination history, the lack of options for biological control (Impson *et al*., 2011), and low current occupancy of its potential distribution (Mgidi *et al*., 2007).

2.2.   Materials and Methods

2.2.1. Study species

Acacia elata is an evergreen, bipinnate tree which under favourable conditions can attain a height of more than 20m (Poynton, 2009). It has an extensive natural distribution in south-eastern Australia and Tasmania, growing best in warm, humid conditions (Poynton, 2009). The size of the tree, dark green leaves, and yellow flowers arranged in racemes make it "Unquestionably one of the handsomest of all the Australian [*Acacia*] species… when at its

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thriftiest, verges in appearance on the majestic" (Poynton, 2009). The species was introduced to southern Africa as an ornamental species several occasions between 1904 and 1940. Introductions were haphazard and spread throughout the region, with small scale plantings in the Western Cape, Eastern Cape, Free State, Gauteng, KwaZulu-Natal and Zimbabwe (Poynton, 2009). The species has since become naturalized and established in many regions of the country and is at present considered an increasing threat, occupying 4.5% of its climatic potential which is estimated as 50% of Southern Africa resulting in it currently being listed under category 3 according to the Conservation of Agricultural Resources Act (Act 43 of 1983) (Nel *et al*., 2004; Mgidi *et al*., 2007).

Acacia elata seeds are black with a thick outside coat with an attached white aril (O'Dowd & Gill, 1986). It has been suggested that secondary dispersal by ants could occur after initial gravity driven dispersed seeds (O'Dowd and Gill, 1986). Seed pods float and thus secondary dispersal along rivers or down slopes in heavy rain is also a possibility. Surveys in Australia attempting to find a host specific biological control agent for this species have so far been unsuccessful (Impson *et al*., 2011). Although successful biological control agents of other *Acacia* species have the potential to affect *A. elata*, the lack of a species-specific control agent means that land managers are limited in their ability to restrict future dispersal events (Impson *et al*., 2011).

2.2.2. Study site

Five *A. elata* stands on relatively flat gradients were selected within the Western Cape, South Africa. Sites were selected with a range of disturbance histories and with different invasive ages (Table 2.1).

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2.2.3. Age at sexual maturity

To estimate age at first reproduction, we cut down fifty of the smallest trees at all sites (i.e. those likely to be the youngest in an invasive stand) that had reproductive organs present and counted age rings.

2.2.4. Seed rain and seed dispersal experiments

Both the seed dispersal and seed rain experiments utilized the seed traps described in Cottrell (2004). Two-litre plastic bottles were cut and the top end inverted and placed in a PVC pipe for support. A mesh bag was attached to the open lid of the bottle to create a net into which seeds were funnelled. The PVC pipes placed in the field and supported with steel pegs to restrict movement (Cottrell, 2004).

At each site, five isolated sexually mature trees were selected for analysis of seed rain. The height, canopy width, diameter at basal height (DBH) and position of every tree was recorded. Five seed traps were placed at the edge of the canopy of each tree, the first trap facing north and the other four traps arranged at 72° intervals around the canopy of the tree. Traps were set at all sites prior to seed rain (pre-dehiscence), in late August 2012, and were checked every fortnight to limit seed loss due to predation until post-dehiscence when traps were collected in early January 2013.

As seed rain measures are counts, generalized linear models (GLM) assuming Poisson errors were used to estimate the log mean seed rain per tree (seeds.m^{-2}; Quinn & Keough, 2002). These were then compared using one way interactions with tree height, DBH and canopy width, with AIC values used to select the best explanatory variable.

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At three of the five sites selected for seed rain analysis, three mature trees with canopy widths of 6m, similar tree height and DBH were selected for analysis of seed dispersal. Seed rain and dispersal in Australian acacias has been shown to be influenced by the dominant wind direction (Marchante *et al.*, 2010). In this study we were interested in the maximum gravity-driven dispersal distances of *A. elata* seeds and therefore set seed dispersal traps on transects extending away from the selected trees in the direction of the dominant wind direction. Dominant wind direction was obtained from the closest weather stations to each site (http://www.windreport.co.za), and we used the value for when seed rain was at its peak, i.e. December. Traps were set out in a regular distribution along one permanent transect for each tree (Bullock *et al.*, 2006; Marchante *et al.*, 2010) resulting in three permanent transects at each stand. Following the method of Marchante *et al*. (2010), the end of the most extreme pod bearing branch was labelled as the zero point with a trap placed at this point. Ten traps were then placed every metre for 10m along the transect running away from the tree. Another three traps were positioned at 1-m intervals for 3m towards the base of the tree stand. Two traps were placed 20m and 50m along the transect line away from the canopy, resulting in a total of 15 traps per tree. Traps were set at all sites pre-dehiscence, in late August 2013 and checked every fortnight to limit seed loss through predation in traps until post-dehiscence when traps were collected in early January 2014.

Seeds per trap were converted to seeds.m^{-2} and corrected for distance from parent tree by multiplying seed density by the area covered at the relevant distance. We analysed the effect of distance from the parent canopy to proportion of seed by regression using a GLM with negative binomial errors to account for overdispersion. The relationship between tree height and seed rain was then used in conjunction with the percentage of seeds falling

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directly under the terminal branches of the canopy to estimate the total number of seeds produced by a single tree of given height.

2.2.5. Seed bank dynamics

Seedbank sampling took place at all five sites both pre- and post-dehiscence during August 2013 and January 2014. To get the most accurate sample of the seed bank with reference to size and spread, random soil samples were collected under the canopies of the five different stands, following the approach developed by Strydom *et al*. (2011). Fifty samples were taken (no closer than 10m to one another) using a cylindrical corer with 7.2cm girth down to a depth of 40cm at each site. The samples were divided into 10cm depth classes i.e. 0-10cm, 10-20cm, 20-30cm, 30-40cm, and kept separately. Each soil sample was sieved through 2mm mesh and the seeds collected and counted. At each sampling position, the associated tree density was calculated using a wedge prism (Jorgen & Karsten, 1994).

The low number of seeds found at depths below 10cm meant that for comparisons between sites data for all depths were combined. The numbers of seeds pre- and post-dehiscence were compared using GLMs with negative binomial errors to cope with overdispersion (Crawley, 2007) for both the seedbank and leaf litter with ANOVAs run to test for significance with any relationships found.

Only sites 1 and 5 had enough seeds below 10cm to allow for comparisons of seed numbers at different depths. For each site generalised linear mixed models with Poisson errors were created with depth as the fixed effect and the core number as random effects. ANOVAs were run to test the significance of any relationship found (Quinn & Keough, 2002).

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2.2.6. Seed germinability and viability

Seeds were collected from both seed rain (fresh) and seedbank (soil stored) experiments and used to test seed germinability, viability and response to fire stimulation. One hundred seeds from the seed rain traps and 100 seeds from soil stored seed for each site were washed with bleach (5%) to avoid fungal infection, and then placed in sterilized glass Petri dishes on water soaked filter paper kept at a constant 25°C. Rotten and germinated seeds were removed every two days for 30 days. After this period, any remaining seeds were considered dormant. The micropylar end of dormant seeds was then cut and seeds left as before until they either rotted or germinated. This process was repeated twice, once with water replaced by smoke primer purchased from the South African National Biological Institute, and a second time with boiling water to simulate conditions during fire, which has been shown to break the dormancy of other invasive *Acacia* species (Brown *et al*., 2003). Seed germinability for the three different treatments and two source seeds was compared using a GLM with binomial errors.

2.3.   Results

2.3.1. Age to sexual maturity

Ten trees were recorded to have sexually reproductive organs at 4 years old; remaining trees (n=40) were between 5 and 8 years of age.

2.3.2. Seed rain and dispersal

As expected, the greatest density of seeds was recorded directly under the canopy close to the stem (**Fig. S2.1**), with seed density declining significantly with increasing distance from the canopy (ANOVA p<0.01). No seeds were found more than 6m from the canopy edge.

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However, after correcting for area, the highest proportion of seed rain was directly under the terminal branches of the canopy (**Fig. 2.1**). Of the seed falling outside of the canopy, 50% of seed was estimated to fall within 3.85m of the canopy (95% CI 3.04-5.25m) while only 5% falls further then 16.64m (95% CI 13.14-22.69, **Fig. 2.1**).

There was a significant relationship between seed rain and tree height, DBH and canopy width, with tree height having the greatest explanatory power (**Fig. S2.2**). We estimate that an average 9m tree in the Western Cape releases around 17000 seeds per annum with large trees (>20m) releasing over 50000 seeds per annum and small trees (3m) around 10000 seeds per annum. The mean seed rain varied between sites from ~100 to 800 seeds.m^{-2} (Table 2.1).

2.3.3. Seed bank dynamics

Leaf litter seed counts increased on average from 804 seeds.m^{-2} (95% CI 571 to 1136 seeds.m^{-2}) pre-dehiscence to 1826 seeds.m^{-2} (95% CI 1300 to 2568 seeds.m^{-2}) post dehiscence (ANOVA p<0.01) (Table 2.1).

The same relationship was not observed in the seedbanks, and no significant relationship was observed between pre- and post-dehiscence seed numbers (ANOVA p>0.05). Only one site (Spanish farm) had seeds down to a depth of 40cm (**Fig. S2.3**), with the majority of seeds found in the top 10cm of the soil (ANOVA p<0.01, **Fig. S2.3**). The highest recorded density for a single core was 95 971 seeds.m^{-2}.

2.3.4. Seed germinability and viability

There was no significant relationship between seed germinability and viability and site (ANOVA p>0.05). Of the seeds that fall from trees, 10.4% spontaneously germinate

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compared to 2.8% of seeds in the seedbank (ANOVA p<0.05). Smoke water had no significant influence on germination (ANOVA p>0.05); however treatment with boiling water resulted in 77% of seeds in the seedbank and seed from seed rain germinating (ANOVA p<0.01). Mean seed viability for all treatments and sites was 97%.

2.4.   Discussion

High seed rain within dense stands of *Acacia elata* results in high annual seed input into the leaf litter, which, combined with high seed viability and high levels of dormancy, creates large seedbanks of similar proportions to those of other invasive *Acacia* species in South Africa (Richardson & Kluge, 2008; Table 2.2). Of all reproductive traits of *Acacia*, persistent large seedbanks pose the greatest difficulty to management and play a substantial role in the ability of invasive populations to respond to natural and management driven disturbances (Richardson & Kluge, 2008; Wilson *et al*., 2011). Thus, it appears that the reproductive traits of *A. elata* are consistent with the species becoming an increasing invasive problem in South Africa.

2.4.1   Age to sexual maturity

One difference between *Acacia elata* and other invasive acacias is that *A. elata* has a longer time to first reproduction (~4 years). Gibson *et al*., (2011) report that *Acacia* species that are able to attain maturity within two years of germination were more likely to become invasive than those that are not. It is possible that the longer time to reach reproduction has slowed the rate of establishment of new *A. elata* populations. Encouragingly, the period between emergence and reproduction gives management a greater opportunity to accomplish follow up operations on cleared sites to ensure seedlings emerging after clearing do not begin new seed production in the area.

2.4.2   Seed rain

The highest recorded mean seed rain for this study (767 seeds.m^{-2}) was within the range reported for two of the most invasive Australian *Acacia* species in South Africa: *A. saligna* (530) and *A. cyclops* (1197) (Milton & Hall, 1981). However, all sites but one examined in this study showed annual seed rain an order of magnitude lower than those recorded for *A. saligna* in the Western Cape by Strydom (2011). It is possible that either pollination (Parker, 1997) or environmental conditions (Strydom, 2011) are limiting the development of seed in the stands assessed in this study. However, our estimates of annual seed production of individual trees (10000 – 50000 seeds.yr^{-1}) are within a similar range to those estimated by Milton & Hall (1981) for Australian *Acacia* seed production in the Western Cape: 9 500 - 48 000 seeds.yr^{-1}. This is likely the result of the large canopies and substantial height of *A. elata* trees which would result in a broad dispersal shadow. Consequently, despite the low density of seeds recorded at the terminal branches, the overall input of seeds from individual trees remains substantial, as seeds falling directly under the terminal branches represent a small percentage of all total seed rain. This is supported by the high seed densities that we noted close to the stem, suggesting that traps placed closer to the stem of the tree would have given greater seed rain densities than those that were measured directly under terminal branches. In addition, seeds captured at 6m from the edge of canopies suggest seed shadows larger than have been recorded for the highly invasive *A. longifolia* in Portugal (Marchante *et al.*, 2010), though this is hardly surprising given the relatively large height of mature *A. elata*. This does mean, however, that large trees grown in protected gardens for long periods can act as seed sources.

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2.4.3   Seed dispersal

Seed dispersal results indicate that the majority of seeds fall within 4 m of the parent canopy while only 5% of seeds are dispersed beyond 16m. In reality the seed shadow is likely larger than this, as detection of seed fall at distances further then 10m was highly unlikely given the low number of traps placed at greater distances (Pielaat *et al*., 2006). Seed dispersal plays a critical role in determining the speed of invasive spread (Kot *et al*., 1996) and it is likely that the potential to disperse seeds over relatively large distances purely through gravity will have played a role in the escape from cultivation and spread of *A. elata* in South Africa. However the distances recorded here are far lower than those associated with secondary movement of seeds by birds and mammals observed in other invasive *Acacia* species (100m+; Glyphis *et al*., 1981). The white arils on seeds suggest that dispersal by ants is possible (O'Dowd & Gill, 1986), but this is unlikely to add to the overall dispersal distances of seed (Bond & Slingsby, 1983; Holmes, 1990; Richardson *et al*., 2000a). In addition, the regional, long-distance movement of propagules that would drive spread of a species at the regional level is likely linked more closely to human-aided dispersal than natural dispersal (Pauchard & Shea, 2006). Thus, although a lack of a secondary disperser may play some role at the stand level of population spread, the regional movement and national distribution on *A. elata* is probably more the result of limited human dissemination as a pose to limits to dispersal distances of individual trees. Taking this into account, observations at sites 2, 3 and 5 (All occurring under pine forest plantations) of trees growing up to 2km from the main invasion foci with no other seed source in the area, suggests that unintentional human movement of seeds in the area is still playing a role in the spread of the species. Similar observations at Lanzerac farm (within a riverbed) will more likely be

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driven by the movement of buoyant pods downstream. These propagules are of the greatest concern to management as their detection and removal has the largest impact on effective containment and/or eradication of populations (Panetta, 2009; Moore *et al.*, 2011). Despite the significant distance over which seeds are naturally dispersed the movements of seeds long distances via secondary dispersal pathways will play a greater role in the overall spread of the species.

2.4.4   *Seed bank dynamics*

The seedbanks found are similar in proportions to those of the other invasive Australian *Acacia* species in South Africa (Table 2.2). Smaller seedbanks at the two Lourensford sites and the Lanzerac site can be attributed to recent fires (young stand age) and flooding within the river system respectively (Table 2.1).

2.4.5   *Limits to current invasive distribution*

Limitations to spread resulting from limited plantings and placement of these initial introduction foci within gardens as opposed to open landscapes (as was the case for species used for forestry or dune stabilization) is more likely to explain its limited extent. However, the longer the species is allowed to persist without any form of control, the more likely that both deliberate and unintentional regional movement of the species will occur, resulting in increased spread and greater economic costs to future management.

2.4.6   *Recommendations for management*

Our findings indicate that young stands have limited seedbanks. If the goal is extirpation, plants should be cleared, a heat treatment used to stimulate seed-germination, and a follow up clearing done within a four year period (Milton & Hall, 1981; Richardson & Kluge, 2008).

It is, however, unlikely that more established stands with large seedbanks can be extirpated without substantial investment in time (Richardson & Kluge, 2008). In such cases, containment may be the best option. The long pre-reproductive period and the ease with which sexually reproductive trees flowering during mid to late summer can be identified would make such management feasible. Populations in areas close to open landscapes with high human activity (e.g. pine plantations) and those in river beds should receive the most intensive management with populations removed in riverbeds where seedbanks do not appear to represent a large obstacle. In order to limit the development of new invasive populations the issue of large seed producing trees in private properties in close proximity to land suitable for spread needs to be addressed. A reproductive feeding biocontrol agent would be highly valuable, both by limiting the build-up of seedbanks, and reducing rates of spread.

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Table 2.1 Measurements of seed production at five *Acacia elata* stands in the Western Cape.

	Latitude	Longitude	Habitat description	Stand age (years)	Last fire	Wind[a]	Mean tree height (m)	Tree density (m² wood/ha)	Seed rain (seeds.m⁻²)	Seed density pre-dehiscence (seeds.m⁻²)	Seed density post-dehiscence (seeds.m⁻²)	Seedbank (seeds.m⁻²)	Estimated annual input[b] (seeds.m⁻²)	Estimated accumulation time[c] (years)
Warwick farm	-33.8442	18.8639	Road side	20 +	Not known	SE	14.46	428	360 (110-610)	1806 (911-3450)	3388 (2620-4292)	21171 (17689-25631)	1375	19
Lourensford 1	-34.0266	18.91177	Pine plantation	5	2009	SE	10.20	431	393 (106-679)	358 (196-634)	975 (793-1183)	287 (220-366)	536	5
Lourensford 2	-34.0258	18.90754	Pine plantation	5	2009	SE	5.60	395	97 (37-157)	315 (135-697)	559 (405-748)	96 (62-140)	332	4
Lanzerac farm	-33.9591	18.9163	Riparian	20+	Not known	SE	9.20	355	363 (111-617)	110 (31-307)	1027 (778-1326)	167 (109-244)	797	4

| Spanish farm | -34.0523 | 18.85765 | Pine plantation | 30+ | Not known | SE | 16.20 | 427 | 767 (388-1145) | 2303 (1019-4893) | 5725 (4303-7429) | 19160 (14958-24082) | 2974 | 10 |

[a] Dominant wind direction for December when seed dispersal trapping was undertaken estimated from the closest weather stations available at http://www.windreport.co.za

[b] Annual input is given by annual seed addition (pot-dehiscence leaf litter minus pre-dehiscence leaf litter) to leaf litter minus seeds spontaneously germinating or unviable.

[c] Accumulation time calculated by $(s/r) + y$ where s = seedbank size, r = annual input and y = years until reproductively active (4 years; Milton & Hall, 1981)

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Table 2.2 The two largest seed banks and seed rain sites recorded for *A. elata* compared with the maximum recorded values of seed rain and seed banks of other invasive Australian *Acacia* species in South Africa (data for other species from Richardson & Kluge, 2008).

Acacia species	Seed rain			Seedbank			Estimated accumulation time for mean seed bank (years)
	Annual seed rain (seeds.m^{-2})[a]	Viability (%)	Dormancy (%)	Seed density (seeds.m^{-2})	Viability (%)	Dormancy (%)	
A. elata (Warwick farm)	1 582	97	90	21171	97	97	19
A. elata (Spanish farm)	3 422	97	90	19 160	97	97	10
A. cyclops	1 977	100	90-98	5 100	99	99	11
A. longifolia	11 500	-	96	34 000	97	98	
A. mearnsii	-	-	-	5 314	83	-	8
A. melanoxylon	3 200	-	-	43 739	70	-	25
A. saligna	5443	98	97	46 000	96-97	96	8

[a] Annual seed rain for other studies was done at the stand level using seed traps, to allow for comparison, seed rain at the stand level for *A. elata* was estimated from the difference between post- and pre-dehiscence leaf litter seed densities
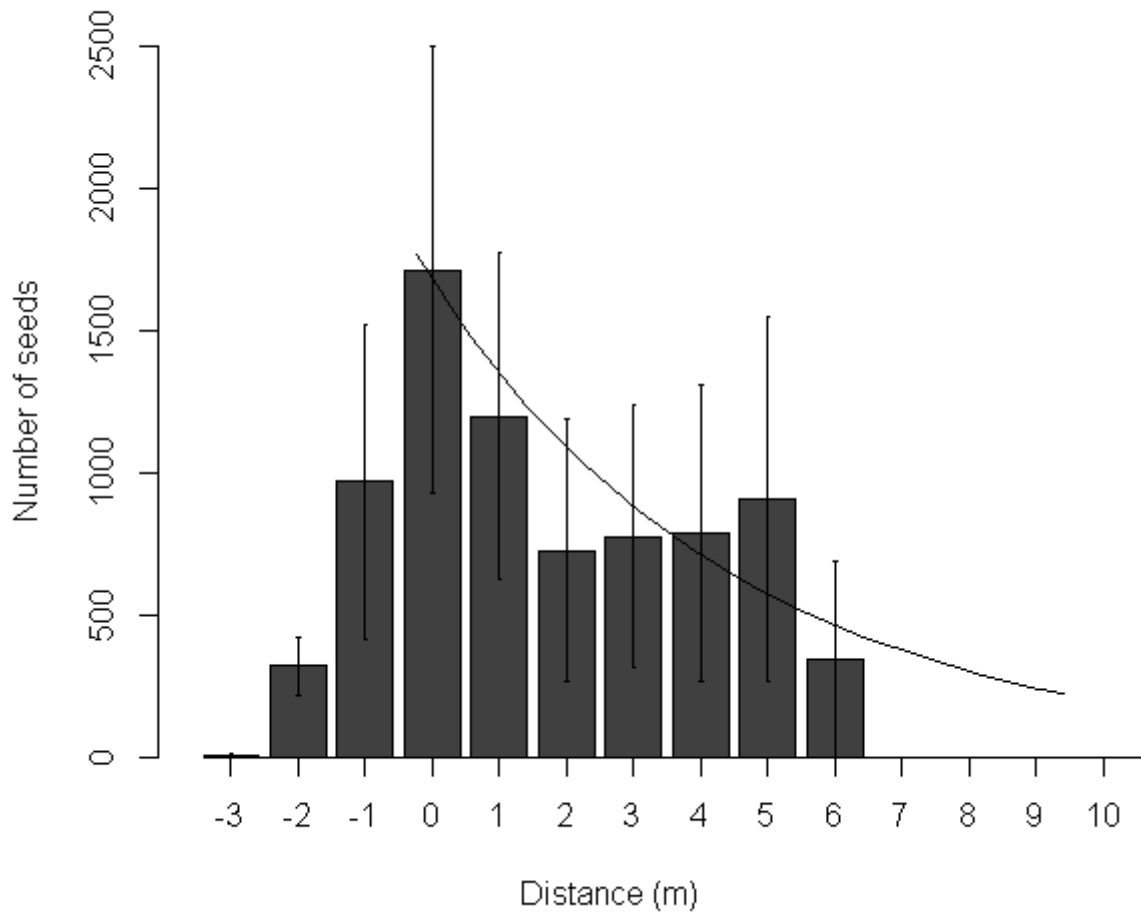
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Fig. 2.1 Seed fall at different distances from the terminal branches (0m) of *Acacia elata* canopies (error bars represent 95% CI). The black line represents the modelled relationship between distance and seed fall from the edge of the canopy outwards.

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Chapter 3: Invasion trajectory of alien trees: the role of introduction pathway and planting history

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Keywords: *Acacia*, **biological invasions, introduction pathway, intrinsic species traits, invasive distributions, niche shift**

Primary Research Article

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Abstract

Invasion patterns are determined by species traits, the recipient environment, and introduction dynamics. The relative importance of each factor, and the changing interactions during the course of an invasion are rarely understood. We consider 11 Australian *Acacia* species introduced to South Africa for commercial forestry, dune stabilization and as ornamental plants, to determine how features of the introduction pathway have shaped their invasion history. Two hypotheses were developed: 1) invasive populations of commercial forestry species and dune stabilization will have a closer climate match between alien and native populations than is the case for ornamental species; 2) introduction type and human-aided dispersal are more important than species traits in determining the extent of invasions, at least initially.

We tested these hypotheses using species distribution models (SDMs) and lattice models. SDMs were developed using records from native, South African and global ranges. Projections were compared to assess similarity between climatic envelopes. A lattice model was generated for an idealised *Acacia* invasion in the Western Cape. Intrinsic traits and introduction types were varied to assess the relative contribution of these factors to abundance and extent over the course of a simulated invasion. Results indicate that invasive populations of ornamental species occupy substantially different climate space from their native ranges. In the early stages of the invasive simulations, the number of trees introduced was the most important parameter influencing abundance and extent. Conditions associated with the reason for introduction dominate the early invasion dynamics. The placement of introduction foci in urban areas associated with ornamental introductions limited the extent and abundance of invasive populations. Introduction conditions surrounding human

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introduction events appear initially to mask the influence of intrinsic species traits and help

to explain the failure and success of species associated with specific human pathways.

3.1.   Introduction

Species with similar human uses will have similar introduction pathways; that is, they should have certain commonalities in the conditions associated with their introduction and dissemination (Lonsdale, 1999; Lockwood *et al.,* 2005; Thuiller *et al.,* 2006). These factors include the position of introduction foci in the landscape, the number and frequency of introduction events, components of propagule pressure, and the effort and resources devoted to establishment (Wilson *et al.,* 2007; Blackburn *et al.,* 2011). Such commonalities should result in distinctive biogeographical patterns in the invasive ranges – a "signature" that may remain discernible for long periods (decades or centuries; Castro-Díez *et al*., 2011).

Hundreds of tree species have been introduced to areas outside their native ranges in the past few centuries for diverse purposes, including forestry, erosion control and stabilization, and ornamentation (Richardson, 1998; Mack, 2001; Richardson *et al*., 2011). Many introduced tree species have become major invaders (see Richardson, 1998; Reichard & White, 2001 and Richardson & Rejmánek, 2011 for reviews). We examine how key dimensions of the introduction pathways for alien trees affect subsequent invasion dynamics.

Trees introduced for commercial forestry are generally selected from regions with similar climates to the target region (Zobel, 1987; Bennett, 2011), and are usually introduced initially in small-scale trial plantings (see Poynton, 2009 for a review of forestry trials in South Africa). When selected for commercial production, however, forestry trees are planted repeatedly over decades in very large numbers over large areas into multiple areas considered climatically suitable for high productivity growth. These features of the introduction pathway afford propagules opportunities to overcome various barriers to

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establishment in the new environment (Richardson, 1998; Richardson & Rejmánek, 2011). Plantings are usually adjacent to natural or semi-natural vegetation, which provides opportunities for spread (**Fig. 3.1**; Richardson, 1998). Tree species used for dune stabilization are selected for their ability to grow in harsh environments with minimal tending, even at the establishment phase, and species from similar climate regimes are again generally favoured. Once populations have established, little or no further effort is given as populations are expected to be self-sustaining. We suggest that climate matching, high propagule pressure and placement in disturbed landscapes could help species overcome barriers to establishment associated with climate and other environmental limits to the native distribution (Lockwood *et al.,* 2005; Colautti *et al.,* 2006). Initial aid in establishment such as deliberate disturbance of the soil, clearing of competing vegetation, or fertilizer addition may negate environmental barriers limiting establishment and growth (Mack, 2005). Similarly, high propagule pressure, constant reciprocal plantings to new localities, and close proximity of introductions to suitable land for spread may aid species in overcoming ineffective dispersal and low seed set (Simberloff, 1988; Lockwood *et al.,* 2009). Thus it could be predicted that forestry and dune stabilization introductions will lead to a relatively high proportion of naturalized and invasive species as a result of the general characteristics of their respective introduction pathways, regardless of the intrinsic life history traits of the species involved (Gravuer *et al*., 2008).

In contrast, the choice of tree species selected for use as ornamentals is often not limited by the need for productivity (Reichard & White, 2001). Species are often planted in small numbers, as individual trees or small populations which means that they can be intensively cultivated. Such nurturing (e.g. in micro-climates such as irrigated, fertilized gardens or golf courses) often protects isolated plants or small populations from environmental

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stochasticity (Reichard & White, 2001; Mack, 2005). As a result, introduced 'source' populations are more frequently found within conurbations. The urban landscape surrounding these populations frequently provides an abundance of disturbed habitat where biotic and abiotic conditions are altered through human interventions such as irrigation, fertilizer application, removal of native vegetation or the creation of heat pockets (**Fig. 3.1**; Deutschewitz *et al.*, 2003; Chytrý *et al*., 2008; Pickett *et al*., 2008). Consequently, the likelihood of introduced populations naturalizing in urban areas is increased as a result of both the increased propagule pressure from additional plantings to sites, and the high level of heterogeneity of habitats and conditions within conurbations (**Fig. 3.1**; Deutschewitz *et al*., 2003; Chytrý *et al*., 2008; Pickett *et al*., 2008; Aikio *et al*., 2011). Despite this higher risk of naturalisation, the fragmented nature of the physical landscape created by urban environments places limits on the spread of these initial populations. Furthermore, the manipulated microclimates within which these populations find themselves may not match the broader climatic requirements of the species, since introductions of ornamentals are seldom preceded by detailed climate matching. It could therefore be argued that invasive populations stemming from ornamental introductions will frequently be found occupying climatically manipulated 'pockets' within a zone of climatic conditions that do not closely match those in their native climatic range. While naturalization may occur at these limited sites within conurbations, there may be limited potential for spread across the broader landscape as a result of the physical nature of urban landscape. Ultimately, the introduction conditions that promote the naturalization and spread of forestry and dune stabilization species will work against ornamental species, with climatic mismatching, low propagule pressure and unsuitable environment for spread intensifying any limiting life history traits and largely negating life-history traits that would otherwise have promoted spread (**Fig. 3.1**;

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Gravuer *et al.*, 2008). This may explain why, even though most alien plants are initially introduced to urban areas, such areas are not overrepresented as sources of spread or invasion hotspots (Aikio *et al.*, 2011).

From these observations it can be suggested that large-scale planting for commercial forestry and dune stabilization will greatly improve the chances of a species becoming established and naturalized, and many trees used for this purpose have indeed become invasive (Avis, 1989; Richardson, 1998; Mack & Erneberg, 2002; Mack, 2005; Richardson & Rejmánek, 2011). On the other hand, inherent features of the pathway of introduction and dissemination of alien ornamental plants should result in a lower proportion of species introduced for ornamentation achieving broad invasive distributions (**Fig. 3.1**).

We developed two hypotheses surrounding the influence of introduction pathways on resultant invasive populations: 1) Forestry and dune stabilization species will have closer climate matches between alien and native populations than ornamental species; 2) introduction type and human-aided dispersal are more important than species traits in determining the invasiveness of alien populations, at least initially.

3.2.   Materials and methods

3.2.1   Study system

Australian *Acacia* species have been disseminated globally for many purposes for more than 150 years (Richardson *et al.*, 2011). Many introductions have led to establishment and spread, resulting in a number of species becoming amongst the most widespread invasive woody plants globally (Richardson & Rejmánek, 2011). The range of reasons for the movement of Australian *Acacia* species from their native ranges and resultant invasions in novel landscapes make the system ideal for investigating patterns of invasiveness linked to

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conditions of introduction. We focussed on Australian *Acacia* introductions to South Africa due to the well documented history of introduction, large number of species introduced, defined reasons behind introduction events, long periods since initial introductions occurred, similarities in reproductive and physiological traits and high quality of distribution data for invasive alien populations (Henderson, 2006; Poynton, 2009; Gibson *et al.*, 2011).

During the 19th and 20th century, at least 80 species of Australian *Acacia* were introduced to South Africa for dune stabilization, commercial forestry and ornamental use (Henderson, 2006; Poynton, 2009; Bennett, 2011; Richardson *et al.*, 2011). Fourteen of these Australian *Acacia* species (most of which have residence times of 100+ years) are currently considered to be invasive in South Africa (Van Wilgen *et al.,* 2011). Of these, four species were introduced for commercial forestry (*Acacia decurrens* Willd. var. *dealbata* Link F. Muell. ex Maiden, *A. decurrens* Willd., *A. mearnsii* De Wild., *A. melanoxylon* R. Br.), four for coastal dune stabilization (*A. cyclops* A. Cunn. ex G. Don., *A. longifolia* Andrews Willd., *A. pycnantha* Benth., *A. saligna* Labill. H. Wendl.), three were introduced in small numbers for forestry trials before the majority of their dissemination took place through the ornamental trade (*A. baileyana* F. Muell., *A. elata* A. Cunn. ex Benth., *A. podalyriifolia* A. Cunn. ex G. Don.), and finally three are known to have become invasive at only a few sites restricted to trial plantings and were not considered further here as available distribution points were far too limited for accurate climate mapping.

For both commercial forestry species and dune stabilization species substantial effort was expended in identifying areas suitable for growth and large numbers of propagules were introduced - see Avis (1989), Poynton (2009) and Bennett (2011) for reviews. In contrast, trees planted as ornamentals such as *A. elata* were often rejected from forestry trials due to

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their poor wood quality before becoming popular garden plants and being planted for their aesthetic value in residential areas (Poynton, 2009).

3.2.2   Distribution records

Occurrence data from Australia for the 11 *Acacia* species was acquired from the Atlas of Living Australia (ALA; www.ala.org.au; accessed 01.08.2012). Based on the descriptions of native and alien distributions for Australia on World Wide Wattle (www.worldwidewattle.com), records were assigned native or alien status. South African records were extracted from the Southern African Plant Invaders Atlas (SAPIA; accessed 25.04.2012). Data for invasions in other parts of the world were a combination of the alien Australian data and records from the Global Biodiversity Information Facility (GBIF, accessed 25.04.2012).

Data were processed to remove duplicate records and those with obvious errors in the coordinate system (e.g. points in an ocean). Records with locality information at a resolution that was coarser than 10' and records before 1960 were removed to ensure the distribution data matched the resolution and time scale of the climate data used in modelling. Records identified as cultivated or growing in manipulated environments and records of populations in microclimates not detectable at a 10' spatial resolution (e.g. along rivers in arid areas) were removed. Cleaned data were regularised to a single record per 10' cell to reducing sampling bias. See supporting information Table S1 for further details of data cleaning.

3.2.3   Species distribution modelling

BIOCLIM (true/false) model builder in DivaGIS v. 7.5.0 was used to match the climate of the relevant distribution records with that of the rest of the world (Busby, 1986). This method is appropriate for assessing the broad climatic potential of invasive species and is not impacted

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by issues related to artificial absence data, taking into account the whole climatic envelope and reducing the risk of over fitting when projecting potential ranges for invasive species (Lobo *et al.*, 2010; Webber *et al.*, 2011). We developed three species distribution models (SDMs) for each species based on different distribution data: (1) native Australian distribution records (i.e. realized native niche), (2) alien distribution records from South Africa (i.e. realized South African invasive niche), and (3) all alien distribution records excluding those in South Africa (i.e. realized global invasive niche). These models were then used to compare climate conditions for the three different regions.

The meteorological dataset used to calibrate models was the WorldClim Version 1.4 (Release 3) 10' resolution gridded bioclimatic raster set (Hijmans *et al.*, 2005; www.worldclim.org; accessed 01.08.2012). For all models the maximum temperature in warmest month (bio05), minimum temperature in coldest month (bio06), and annual rainfall total (bio12) were used to train and project the models. Only three variables were selected as increasing the number of variables reduces the predicted range and can lead to over fitting (Rödder & Lötters, 2009; Peterson, 2011). The Pearson correlation coefficient was used to ensure that the selected bioclimatic variables were not highly correlated to one another (all were < 0.6).

To identify whether different pathways of introduction impacted the climatic space occupied by invasive populations when compared with native populations (Hypothesis 1), we compared projections for each species using the three different model groups. To compare the overlap between the projections made to South Africa with the three datasets we used ENMTools v.1.3 (Warren *et al.*, 2010) to calculate Schoener's (1968) D index and the Hellinger-based similarity statistic (I) (Van der Vaart, 1998) for each cell. Both measures give a value between 0 (no overlap) and 1 (complete overlap).

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3.2.4 Lattice model of Acacia expansion in South Africa

The lattice model was developed for the Western Cape province of South Africa, where all 11 selected *Acacia* species currently occur. A 1km-resolution binary climatic suitability projection of the Western Cape was generated using known distribution data to create a reasonable degree of realism regarding the connectivity of climatically suitable land available for invasion (see SI for detailed explanation). The percentage of available land for invasion within each 1-km grid cell was calculated using 30m-resolution National Landcover (2009) maps from South African National Biodiversity Institute (SANBI; Fairbanks *et al.*, 2002). Only pixels defined as natural and degraded were considered available for population growth, while cultivated, urban built-up, water bodies, plantations and mines were considered unsuitable. The maximum number of trees that a fully saturated 1km^2 cell could contain was estimated from Veldtman *et al.*, (2010) at 83 893 trees. The product of this value and the percentage of available land determined the carrying capacity (K) for any given cell.

We developed the lattice model on 1-km grid cells to simulate the population dynamics and range expansion of an idealized Acacia species in the Western Cape taking demographic coefficients from literature, as well as different initial propagule sizes (Table 3.1) and dispersal strategies (Table 3.1). In each three-year time step (representing the generation time from seed to adult tree) the tree population within a km^2 cell first undergoes reproduction, then dispersal, and finally population growth up to a set carrying capacity. We did not explicitly include mortality as the substantial seed banks that develop under mature *Acacia* stands means that any adults that die are usually replaced (Wilson *et al.*, 2011). The potential number of new adult trees produced per cell is determined by n × r, where n is the current population size with the cell and r (Table S2) the number of reproductive trees that a single tree can produce during one time step (i.e. 3 years). These potential individuals either

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remain in the same cell (≥97.9%), move to adjacent cells (l_d<0.6~2.5‰; considering 8 neighbouring cells), or are dispersed across the region (G_d<0.1~1‰). Regional dispersal was included to represent the extreme long-distance movement of seeds by humans (both deliberate and accidental). We therefore weighted the likelihood of a cell receiving a seed through regional dispersal by the human influence index of each cell, as calculated in the Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Sanderson *et al*., 2002). The population size will stop growing once its carrying capacity is reached.

For each simulation, abundance was calculated as the sum of the population size in all cells, while occupancy was the proportion of suitable cells that had an abundance >1. Simulations were run five times for each set of parameters (Table 3.1) resulting in a total of 810 runs with every available combination used. To account for the expectation that plant invasions will only reach a broad scale equilibrium with suitable climate in South Africa over centuries, (Aikio *et al*., 2010) as well as the estimated time of introduction for the majority of Australian *Acacia* species to South Africa (Poynton, 2009), simulation models were run for 150 years (50 time steps).

To test the influence of parameters associated with introduction conditions (propagule pressure, placement within the landscape and human aided long-distance dispersal) and species-specifc traits (reproductive rate, local seed dispersal) on abundance and occupancy of populations through time (Hypothesis 2), linear models were fitted for log abundance and occupancy with propagule pressure, placement within the landscape, global dispersal, reproduction rate and local dispersal as explanatory variables (full model). Parameters were then removed systematically (reduced models) and the residuals of the resultant models

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used to calculate the partial correlation coefficient of each parameter (Quinn & Keough, 2002) using the formula:

$$R^2 = \frac{\text{deviance (reduced model)} - \text{deviance (full model)}}{\text{deviance (null model)} - \text{deviance (full model)}}$$

, where R^2 is the coefficient of partial correlation and was used as a proxy for the relative importance of each variable and calculated for each time step. Reduced models were compared to full models using a one-way ANOVA to test whether differences were significant (Quinn & Keough, 2002).

To assess the influence of placement of introduction events (*i.s*) in the landscape on the point at which different management thresholds were reached, we used estimates by Moore *et al*. (2011) that eradication of *Acacia paradoxa* infestations is only cost effective below 777 ha, and containment is only cost effective between 777 and 2500 ha; above this maintenance management is most cost effective. Estimates were made for abundance, assuming that each tree occupied an area of 12 m^2 (maximum carrying capacity of is taken to be ~84 000 trees.km^{-2}). In order to estimate the influence of the placement of populations in the landscape on the time until each threshold was reached, propagule pressure needed to be controlled. To achieve this, the number of trees introduced, data was split into low (2 trees) and medium (1000 trees) introduction events, with high (K trees) excluded as K varied by site and could thus not be controlled. Linear models were fitted to the relationship between time taken for populations to reach thresholds and the remaining parameters (full model). Parameters were then removed systematically (reduced models) and the residuals of the resultant models used to calculate the relative model importance of the placement of introduction points (Quinn & Keough, 2002). Reduced models were compared to full models

using a one way ANOVA to test whether differences were significant (Quinn & Keough, 2002).

3.3.   Results

3.3.1   Human-mediated introductions dictate the extent of climate similarity

Model projections based on native range records for South Africa for all ornamental species indicated minimal areas of climatic suitability in South Africa. However, models calibrated with South African distribution data indicated that populations in this part of the alien range occupied large climatic niches. Niche-overlap tests indicate that models calibrated with South African data and those calibrated with native data had consistently lower niche overlap for ornamental species than forestry and dune stabilization species, with almost no overlap and similarity between the native and alien niches of ornamental species (Table 3.2). Dune stabilization species had relatively low niche similarity between South African and native models, with *A. cyclops* and *A. saligna* occupying a wider climatic niche in the introduced South African range than in the native range and having the least similarity between the native and invasive range. Forestry species had consistently high overlap between South African and native models, with the South African models of *A. dealbata* (D=0.698, I=0.788) showing the greatest similarity with the relevant native models and *A. mearnsii* (D=0.490, I=0.694) the lowest similarity and largest projected area for the South African model (Table 3.2). These results were largely mirrored with comparisons between native models and those calibrated with global invasive distribution records (Table 3.2).

3.3.2   Simulated Acacia expansion in South Africa

Increases in the number of trees introduced, global dispersal, reproductive rate, and local dispersal all had positive effects on occupancy and abundance over time (ANOVA p<0.001).

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Dune plantings with 2 initial trees and 1000 initial trees shorten the time taken for populations to reach both management thresholds when compared with ornamental plantings of the same scale (ANOVA, P<0.001) except at the lowest reproductive rates. The introduction scenario had the greatest influence (21%) on populations where the number of trees introduced was low (2) and decreased to (8%) when introductions were larger (1000). In all simulations, populations with initial conditions set to ornamental introductions took longer to reach management thresholds than their corresponding dune plantings (**Fig. 3.2**).

In the early stages of the simulated invasions, the number of trees introduced was the most important parameter influencing the number of cells occupied and abundance. However this initial influence decreased over time to less than 3% and 7% after 150 years for occupancy and abundance, respectively. Global dispersal had the greatest cumulative importance over the 150 years for occupancy. However its relevance to abundance was lower, only being greater than 5% after 97 years and never becoming greater than 10%. For both occupancy and abundance, the reproductive rate increased in importance with time as populations grew, with the largest cumulative importance over the 150 years for abundance, and a relative importance for occupied cells of 51% after 150 years (**Fig. 3.3**). The local dispersal had the smallest influence on occupancy and abundance over the entire simulation. Introductions to areas typical of ornamental plantings negatively influenced the number of cells occupied and abundance when compared with dune introductions (ANOVA, P<0.001). This impact on occupancy is consistently greater than 5% for the first 57 years of simulations, decreasing to less than 1% after 126 years (**Fig. 3.3a**). The abundance was influenced to the greatest extent between 20 and 80 years by the area of introduction, with relatively little impact (<5%) over the first 10 years of simulations (**Fig. 3.3b**).

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3.4. Discussion

Our results show (i) that the pathway whereby a species is introduced and disseminated in the new region influences both the population dynamics and the landscape within which a novel species finds itself, and (ii) that, in certain situations, these introduction conditions will have a major initial influence on the ability of species to initially establish and spread in the new habitat, with differences in species traits only becoming apparent later in the invasion event.

3.4.1 *Human-mediated introductions dictate the extent of climate similarity*

The large overlap between the climatic space occupied by alien forestry species in South Africa and their respective native ranges in Australia is largely to be expected, due to the substantial effort put into finding and placing forestry trees (Poynton, 2009; Bennett, 2011). The lower overlap in climatic space observed with *Acacia mearnsii, A. cyclops* and *A. saligna*, when compared to the other forestry and dune stabilization species, is likely due to these species being exposed to a much greater level of human-aided dispersal within South Africa (Poynton, 2009). The resultant alien populations in South Africa will thus have had the opportunity to access climatic space that may not be currently available to native populations due to dispersal and other biological limitations and thus occupy a slightly different climatic space to the native populations (Soberon & Peterson, 2005; Fitzpatrick *et al.*, 2007; Soberon, 2007; Gallien *et al.*, 2010). Similarly, we argue that the lack of similarity between the native and alien range of ornamental *Acacia* species is based on the complex make up of urban landscapes and conditions associated with ornamental plantings (Deutschewitz *et al.*, 2003; Mack, 2005). It is likely that climatic mismatches experienced by ornamental *Acacia* species in South Africa have to some extent limited their invasive

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distributions to disturbed areas surrounding conurbations when compared to the broadly invasive forestry species placed within suitable climate conditions.

3.4.2   Simulated Acacia expansion in South Africa

In the initial phases of our lattice simulation, propagule pressure had the largest influence on both the abundance and occupancy. The effect of propagule pressure was present throughout the 150-year simulation, indicating that differences in propagule pressure can have lasting impacts on the rate of spread and abundance of invasive populations. This is unsurprising as the importance of propagule pressure in invasions has been emphasized previously (Lockwood *et al.*, 2005). The finding that the initial number of trees introduced still has an influence on the invasive population after 150 years supports the findings of Castro-Díez *et al*. (2011) that human-use still largely explained invasive abundance and distribution of *Acacia* in South Africa. The implication is that large scale (high interest) introductions of potentially invasive species result in disproportionately large invasive problems as a result of compounding effects i.e. with each generation, new reproductive plants (interest) are added to the current (principle) source population to generate the following population and thus the size of original population will have long lasting effects on the overall invasive population. The simulation results suggest that the current issues being faced by management in South Africa dealing with invasive species originally introduced for forestry and dune stabilization is likely still a product of the substantial numbers of trees initially introduced to drive the trade that subsequently increased in number every generation, compounding any invasive issue with time. Such insights are useful to management as an understanding that failing to deal with seemingly minor invasive populations now may result in invasions incommensurate with the original problem at a later stage will aid in gathering support for management programs of current invasive

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populations as well as identify pathways that may lead to similar problems in the future. For example, the demand for biofuels in South Africa is likely to lead to the introduction and/or dissemination of a range of different alien woody plants. Knowing how introduction pathways and cultivation practices influence the potential for future invasion dynamics will be useful for planning (Richardson & Blanchard, 2011).

In addition to propagule pressure, the area to which a species is initially introduced in the novel region will be dictated by their introduction pathway (i.e. forestry species in plantations in open areas, dune stabilization species along coastal drift sands in open areas and ornamental plants in human settlements; Wilson *et al*., 2007, 2009). Our simulation model was limited to estimates of available land to assess the influence of where species are introduced. This will no doubt underestimate the limits placed on ornamental plants in urban areas where habitat fragmentation, frequent clearing and intensive management are likely to impose further restrictions. Nevertheless, our results support the idea that both population growth and spread are influenced by the position of introduction foci in the landscape. The model suggests that limits resulting from reduced carrying capacity in urban environments occur most severely between 20 and 50 years, however model limitations mentioned above exclude more severe limits likely to occur during the early stages of invasions. The result of limits stemming from ornamental plantings indicates consistently longer periods taken for ornamental invasive populations to reach management thresholds when the initial numbers of trees are equal.

The combination of low propagule pressure and landscapes that inhibit spread is likely to have played a significant role in the larger invasive distributions of *Acacia* species used for forestry and dune stabilization in South Africa than those used for ornamentation. This is not

to say that ornamental species do not pose a major threat as invasive species. The random position and increased number of foci that will stem from multiple ornamental introductions will limit the ability of management to accurately locate and manage invasions resulting from ornamental introductions, which increases the costs of management and decreases the scale of invasions that can be effectively dealt with, making ornamental introductions more complicated to manage than those attributed to other forms of introduction (Foxcroft *et al.*, 2008; Moore *et al.*, 2011). Furthermore, simulations indicate that ornamental species with high reproductive rates may be able to overcome limitations linked to propagule pressure and the physical landscape over long periods. This is cause for concern considering that many ornamental species are selected for their reproductive traits, such as early flowering age, long flowering times and high seed set (Anderson *et al.*, 2006).

It is also worth noting the importance of long-distance human-mediated dispersal on the spread of invasive populations. Again the simulations indicated that a human-induced dispersal pattern in the form of seed movement over large distances had a substantial influence on the invasive dynamics of populations. Unlike propagule pressure and the placement of populations in the landscape, the effect of long-distance dispersal on occupancy was constant throughout the 150-year simulation period. Again, this seems to support the idea that conditions of introductions resulting from human influences may play a larger role in the scale and distribution of invasive populations than intrinsic species traits and traits related to natural seed dispersal. While the natural dispersal of forestry, dune and ornamental plants may play some role in their ability to escape cultivation, our simulations suggest that the long-distance movement of popular plants by humans will play a greater role in the severity of alien invasions. This is due to the increase in the number of introduction events occurring, which increase the potential to encounter areas suitable for

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'escape' and spread while at the same time increasing both the propagule pressure and number of foci (Dehnen-Schmutz *et al.*, 2007; Foxcroft *et al.*, 2008). These results concur with the findings of Dehnen-Schmutz *et al.* (2007) that trends in the invasive success of ornamental plants in Britain correlate with market popularity and suggest that an understanding of market trends may improve our ability to predict future invasions.

It is likely that following their initial introduction and planting, long-distance dispersal of forestry species also played a key role in the substantially larger invasive distributions of forestry *Acacia* species when compared to ornamental *Acacia* species in South Africa. This is due to the constant movement and reintroduction of forestry species to areas around the country considered suitable for commercial growth (Poynton, 2009). While ornamental plants may be moved long distances on occasion as a result of private interest, the deliberate, commercially driven, mass movement of forestry propagules has probably been much greater than that facilitated by the trade in trees for ornamentation. As a result the invasive distribution of forestry species within South Africa is substantially higher, as would be expected based on model simulations.

Introduction conditions associated with major pathways of tree introductions strongly influence both the ability of the introduced species to establish and then spread. Environmental limitations experienced by ornamental plants are often mitigated by intense cultivation that results in trees being placed in landscapes that enhance their survival but restrict their immediate population growth. This, and the low propagule pressure and placement within the physical and climatic landscape, at least partially explains the long time periods between introduction and invasion for many ornamental species (Kowarik, 1995). Ultimately it appears that introduction conditions dictated by human requirements play a

greater role in the initial phases of an invasion event than intrinsic species traits and that these conditions continue to have an influence over long time periods. This, in conjunction with an understanding of why species are being introduced should be taken into consideration by management attempting to limit current, and restrict future invasions.

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Table 3.1 Explanations for the five adjusted parameters in the model simulation of *Acacia* invasions in the Western Cape, South Africa (Avis, 1989[1]; Poynton, 2009[2]; J.E. Donaldson unpubl. data[3]; Milton & Hall, 1981[4], Marchante *et al*., 2010[5], J.H. Hoffmann and F.A.C. Impson, unpubl. data[6])

Parameter	Definition	Values
Introduction scenario	Placement of the seven source populations within the landscape. Positions were altered to represent dune stabilization introductions into open areas or ornamental introductions into residential, highly populated regions.	See SI Table 2 for coordinates[1,2,3]
Trees introduced	The number of trees introduced to each of the seven source cells at t_0.	low (2), medium (1000), high(4220)[1,2]
Reproduction rate	The number of trees generated by a single tree at each time step (t).	low (0.2), medium (0.6), high(1)[4,5,6]
Local dispersal	The proportion of effective dispersal reaching the 8 cells immediately adjacent to the source cells at each time step (t).	low (0.005), medium (0.009), high(0.02)[4,5]
Global dispersal	The proportion of effective dispersal assigned to global dispersal at each time step (t).	low (0.0001), medium (0.01), high(0.1)

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Table 3.2 Bioclimatic niche similarities of Australian *Acacia* species introduced to South Africa. Overlap in climatic niches was calculated with Schoener's D index and similarity calculated with the Hellinger-based similarity statistic from model projections to South Africa built using native, South African, and global invasive distribution records (both measures range from complete (1) to zero (0) overlap).

Reason for introduction	*Acacia* species	South Africa vs. Native	Native vs. Global
		Schoener's index (D)/Hellinger similarity statistic (I)	Schoener's index (D)/Hellinger similarity statistic (I)
Ornamental (n=3)	A. baileyana	0.000/0.019	0.000/0.019
	A. elata	0.084/0.289	0.117/0.297
	A. podalyriifolia	0.050/0.216	0.135/0.367
Forestry (n=4)	A. dealbata	0.698/0.788	0.137/0.300
	A. decurrens	0.610/0.688	0.399/0.495
	A. mearnsii	0.490/0.694	0.422/0.535
	A. melanoxylon	0.616/0.785	0.692/0.736
Dune stabilization (n=4)	A. cyclops	0.180/0.407	0.177/0.396
	A. longifolia	0.224/0.474	0.277/0.494
	A. pycnantha	0.300/0.541	0.499/0.706
	A. saligna	0.151/0.389	0.110/0.326

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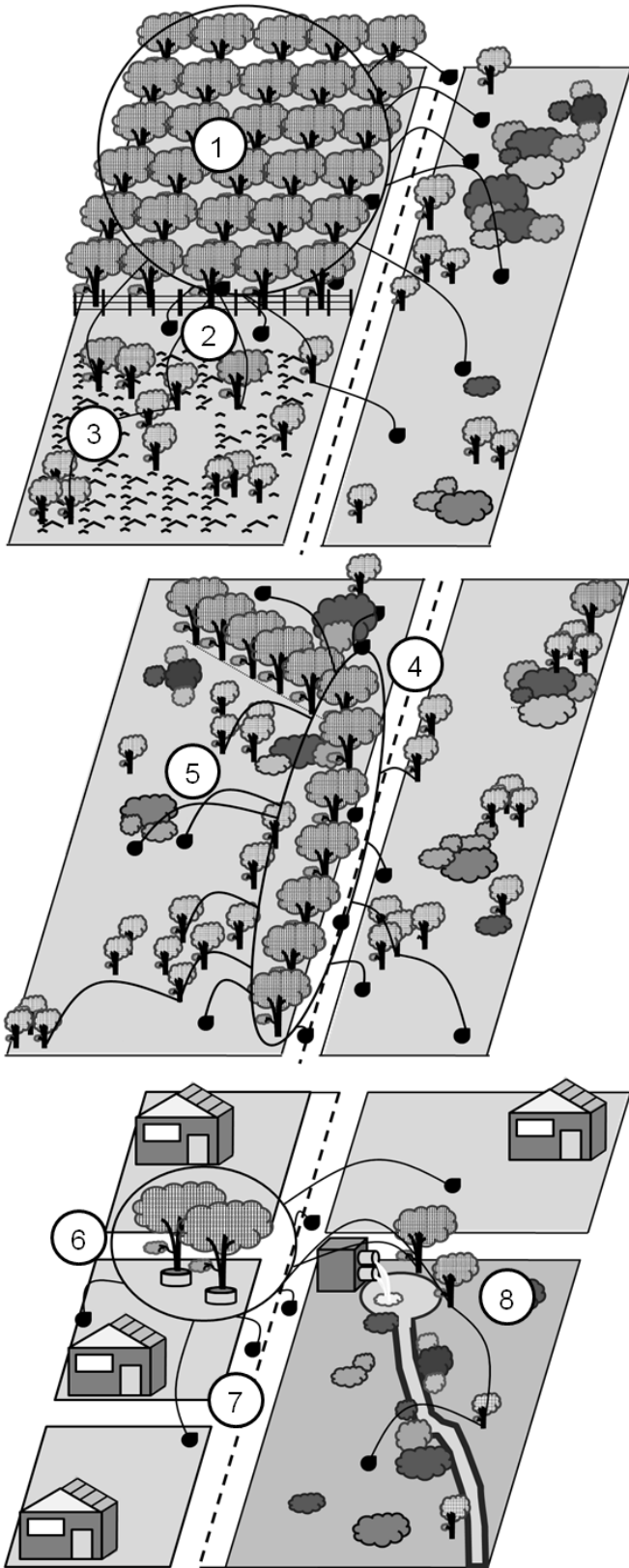
1-Large numbers of initial introductions associated with forestry plantings result in high propagule pressure associated with the subsequent seed rain.

2-Attempts to limit spread of planted trees in the surrounding landscape and natural limitations will result in the majority of seeds not establishing novel populations (black spots).

3-However, the chance of successful establishment will be increased by the proximity of the plantation to disturbed and open habitats in climates that support growth.

4-Dune stabilizing species are planted in high numbers to protect infrastructure, stabilize mobile dunes and disturbed systems.

5-The high propagule pressure, placement within areas that are expected to support growth, and introduction within or alongside open landscape will promote naturalization and spread.

6-Ornamental trees planted in suburban areas will be buffered from environmental fluctuations that would otherwise result in the extinction of small populations under natural conditions by intensive, localized cultivation.

7-Small populations will act as long term seed sources to the surrounding landscape. However the combination of weak propagule pressure and limited suitable habitat in the immediate surroundings will severely limit successful recruitment.

8-The majority of seeds will fail to establish (black dots), however the high heterogeneity of the urban landscape may provide artificially modified, highly disturbed micro-habitats, either intentionally or otherwise, such as irrigated areas and areas of high nutrient input that do support small naturalized populations, despite the potentially unsuitable broader climate.

Fig. 3.1 Schematic representation of the role of introduction history in mediating invasions of alien trees (graphical depiction inspired by Mack, 2005).

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Fig. 3.2 Comparison of the time taken for dune and ornamental simulated populations to exceed eradication estimates (777ha) considering three different initial population sizes (2, 1000, carrying capacity (K)) and reproductive rates.

Fig. 3.3 Relative importance (percentage deviation) of the five simulation parameters (initial number of trees introduced; introduction scenario; reproduction rate; local dispersal; and global dispersal) in determining occupancy (a) and abundance (b) over the 150-year simulations.

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Chapter 4: Scale area curves reveal importance of planting history in shaping the national-scale distribution of an invasive tree

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Abstract

Scale-area curves are increasingly used in ecology to predict population trajectories, based on the assumption that observed patterns are indicative of population dynamics. However, for introduced species, scale-area curves might be strongly influenced by introduction history. We examined the spatial structure of an invasive tree species (*Acacia elata*; Fabaceae) introduced to South Africa as an ornamental plant. A fractal sampling method was used to map the occupancy of *A. elata* at twelve spatial scales for 10 quarter-degree grid cells throughout South Africa. Based on the fractal dimension (D_{ij}) calculated at different spatial scales we found that populations were more contiguous at small (2.5–25m) and large scales (2.5–25km) than at landscape scales (0.025-2.5km). We suggest that natural processes of reproduction and dispersal dominate at the plot scale; at landscape scales invasion foci are more dispersed as tree plantings are scattered around the landscape; while at the broadest scale populations are clustered next to urban areas. This contrasts with another species introduced for dune stabilisation (*A. longifolia*) that has a more consistent pattern across all spatial scales, the sort of pattern theoretically linked to rapid population expansion. We conclude that introduction patterns and human-mediated spread will likely have long-lasting impacts on the patterns observed in scale-area curves, and that these factors may obscure a strong signal of an expanding population.

4.1 Introduction

Local population abundance and broad-scale range extent have been shown to be positively correlated for numerous taxa in multiple regions (Gaston, 1999). However, variation in the relationship between abundance and extent can provide rich information on the distribution and spatial dynamics of a population. Scale-area curves are an elegant way of extracting important information from available data; they involve predicting species abundance by projecting the occupancy–scale relationship across multiple scales down to a 'micro' scale which incorporates single individuals (Hartley & Kunin, 2003; Hartley *et al*., 2004; Hui *et al*., 2009; Hui, 2011). The slope of area occupied and linear resolution give information on the space filling properties of populations over a given range of scales (Hartley *et al*., 2004; Hui *et al*., 2009; Hui, 2011), with steep slopes representing fragmented populations and flatter gradients reflecting contiguous populations (Kunin, 1998; Wilson *et al*., 2004). Thus, scale-area curves can be used to estimate the abundance of a populations (Kunin, 1998; Hui *et al*., 2009) which can in turn be used to estimate the probability of range expansion and contraction in species – those with steep scale-area curves may be expected to be in decline while those with flat curves are expected to expand (Wilson *et al*., 2004).

The ability to predict and understand the expansion and spatial structure of a species at different spatial scales is, of course, of substantial value in understanding and controlling invasive species (Pauchard & Shea, 2006). For invasive species, the occupancy-abundance relationship implies that if a species increases its local abundance post introduction it can be expected to increase its range (Gaston, 1999). In established invasive populations it has been argued that an increase in abundance at the edge of their current range indicates future spread is likely (Arim *et al*., 2006; Veldtman *et al*., 2010). Despite the value of abundance data for gaining insights on many aspects of biological invasions, data are seldom available at

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the level of resolution required for detailed analysis (Gaston, 1999; 2008). One solution is to sample at multiple resolutions and use scale-area curves to predict invasive threat and potential of a population to spread (Veldtman *et al*., 2010).

Studies comparing species that have become invasive and those that have failed have identified many factors that mediate the success of introduced species in the novel range (Lonsdale, 1999; Lockwood *et al*., 2005, 2009; Thuiller *et al*., 2006; Castro-Diez *et al*., 2011; Zenni & Nunez, 2013). These include the position of introduction foci in the landscape, propagule pressure, and the extent of human usage (Wilson *et al.*, 2007). These factors can all be linked to events and practices associated with introduction history (Thuiller *et al*., 2006). Consequently, it has been argued that invasion patterns can be better described by factors that have shaped their introduction than by intrinsic species traits (Lonsdale, 1999; Lockwood *et al*., 2005; Thuiller *et al*., 2006; Wilson *et al*., 2009; Castro-Diez *et al*., 2011; Procheş *et al*., 2012). Therefore, invasive species introduced in similar ways (i.e. for similar human uses) should have similar spatial patterns (Castro-Diez *et al*., 2011). Moreover, most invasive species have not reached an equilibrium state within the new region (Rouget *et al*., 2004) which means that observed scale-area curves should be strongly influenced by the human-mediated introduction history. Ignoring the influence of human history in shaping spatial patterns of invasive populations could lead to inappropriate management decisions. For example, species planted recently may be experiencing local-scale processes highly conducive to spread. However, being in the early phase of invasion, the signature of human-dictated placement at scattered localities may suggest that the species is fragmented, in decline and/or of minor importance (cf. Wilson *et al*., 2004).

Plants selected for use as ornamentals are often planted in small numbers, as individual trees or small populations (Mack, 2005), with most plantings around human

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settlements (Deutschewitz *et al.*, 2003; Foxcroft *et al*., 2008). Invasive populations stemming from these introductions will occur predominately within these same conurbations. Therefore ornamental plantings will likely appear fragmented at the broad scale, at least in the early phases of an invasion. Moreover, while the urban landscape may provide areas of disturbance and protection from stochasticity as a result of human activity (Deutschewitz *et al*., 2003; Chytrý *et al*., 2008), the fragmented nature of available land within urban landscapes might further impose a spatial structure on any invasive populations. This is in contrast to other methods of introduction such as the introduction of trees for silviculture where continuous broad-scale stands are typically planted over large areas with numerous introduction sites in regions of close proximity to one another (Richardson, 1998; Richardson & Blanchard, 2011). Invasions stemming from such introductions may be expected to have a contiguous spatial structure at the landscape scale (e.g. Richardson & Brown, 1986). Human-usage factors at the stand level would therefore play a reduced role and thus the spatial structure of specific stands should be a representation of natural spread rather than an artefact of human introduction.

Previous research on the distribution of invasive *Acacia* species in South Africa used scale-area curves at multiple scales to facilitate the assessment of the invasive risk of species in different habitats (Veldtman *et al*., 2010). However, this work focused on well-established invasive populations of a species introduced and disseminated mainly for dune stabilisation that has likely overcome limitations to its distribution related to human-mediated dispersal. Here we identify and analyse the spatial pattern of an invasive *Acacia* species disseminated as an ornamental tree that is likely to still exhibit spatial patterns in its distribution related to the method of introduction.

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Acacia elata (A. Cunn. Ex Benth.), one of at least 80 species introduced to South Africa (Richardson *et al*., 2011), was initially used in trial plantings for silviculture in the early 20th century (Poynton, 2009). However, the species failed to impress for its original intended use, and instead became a popular garden plant and was widely disseminated as an ornamental plant. *Acacia elata* was therefore introduced over broad regions in small numbers to multiple centres of human habitation across the country (Poynton, 2009). It has since become naturalized and invasive in a number of regions but to date has received little direct management attention. Ongoing research has shown that reproductive biology of *A. elata* is not limiting its invasion in South Africa, although dispersal is mostly through gravity, and so seeds do not naturally disperse particularly far (99.9% <20m; **Chapter 2**). Here we describe the spatial structure of invasive populations of *A. elata* in South Africa using scale-area curves and test two hypotheses:

1) At the smallest scale, invasive stands of *A .elata* will be dense;

2) At regional scale, invasive stands of *A. elata* will be fragmented, reflecting the pattern of initial plantings.

4.2 Material and methods

We followed the methodology of Veldtman *et al*., (2010). Quarter-degree grid cells (QDGC, 15' latitude by 15' longitude) occupied by *A. elata* were identified using the Southern African Plant Invaders Atlas (SAPIA). Ten QDGCs were selected to incorporate cells from the entire range of occupied cells across the range of the species in South Africa. Cells were described as suitable (>50%) or unsuitable (<50%) depending on the proportion of area within the cell predicted as suitable by the climate suitability model generated using invasive distribution data (**Chapter 3**). Eight suitable and two unsuitable cells were selected (**Fig. 4.1**) for fractal sampling field surveys (Kunin, 1998; Hartley *et al*., 2004; Veldtman *et al*., 2010).

4.2.1   Fractal Sampling

Each selected QDGC was divided into 100 equally sized cells (1.5' by 1.5') which were systematically surveyed. Within each cell the presence or absence of *A. elata* was noted and the abundance within the cell estimated as low (<10 individuals), medium (10< *x* <100) or high (>100). Where possible, one high and one low abundance cell were selected and split into a further 100 cells (0.15' by 0.15') and the process repeated before two 0.15' by 0.15' cells were selected and divided into 100 cells (0.015' by 0.015'). The abundance in these cells was identified as low (<10), medium (10< *x* <50) or high (>50) and, where possible, two cells of each category randomly selected. The six randomly selected cells were then split into 100 cells each and the number of trees within each cell with a circumference of greater than 150mm counted (**Fig. 4.1**).

4.2.2   Generating scale-area curves

We constructed scale-area curves by comparing the linear occupancy (km^2) and linear resolution (km). Longitude was converted to the appropriate distance in kilometres using the equation: Longitude = (pi/180) * R * cosA,

where R represents the radius of the earth and A represents latitude. Across the study area (26°S–35°S) the longitudinal length of cells varied 25.2–26.1 km, with a constant latitudinal length of 27.6 km. Occupancy was determined at each scale by multiplying the number of occupied grid cells by the size of the cell (Hartley *et al*., 2004). Occupancy was estimated at four different resolutions by aggregating the finest resolution data (100cells) into three levels of coarser resolution (25cells, 4cells and 1QDGC; also see Veldtman *et al*., 2010). As a result we analysed occupancy at 12 fractal dimensions (*sensu* Veldtman *et al*., 2010; Hartley *et al*., 2004; Wilson *et al*., 2004) (scales i–j in approximate km: plot scale, 0.0025–0.005,

0.005–0.0125, 0.0125–0.025; local scale, 0.025–0.05, 0.05–0.125, 0.125–0.25; landscape scale 0.25–0.5, 0.5–1.25, 1.25–2.5; and regional scale, 2.5–5, 5–12.5, 12.5–25).

For each of the 10QDGCs sampled during field work we computed the relationship between the box-counting fractal dimension (D_{ij}) and scale (i-j km). The fractal dimension (D_{ij}) was calculated using the equation $D_{ij} = 2$-b_{ij}, where b_{ij} represents the slope of the regression between log area of occupancy (km^2) and log linear dimension (km) (Hartley *et al.*, 2004). D_{ij} is used to describe the spatial makeup of a species between scales i-j with the maximum value of 2 indicating coarse cells are completely filled with occupied fine scale cells, while a minimum value of 0 indicates the occupancy of a coarse scale cell by a single occupied fine scale cell (Kunin, 1998).

4.2.3   Statistical analysis

All analysis was carried out in R3.01 (R Core Team 2013). Differences between population structure at four different scales (plot, local, landscape, regional) were assessed by comparing all QDGC D_{ij} scores using the Friedmans Rank Sum Test with scale (Hollander & Wolfe, 1999). Post-hoc analyses on Friedmans Rank Sum Test are considered weak (Baguley, 2012). To test for interactions between different scales we therefore rank transformed data before analysing them using a one-way repeated measures ANOVA with scale the within-subjects-factor grouped by QDGC. A post-hoc Tukey HSD test was then run to assess where differences in spatial structure between scales occurred (Conover & Iman, 1981; Baguley, 2012).

To compare the spatial structure of *A. elata* with that of *A. longifolia* we used data for the 8 cells occupied *A. elata* QDGCs with the 12 cells occupied by *A. longifolia* (data from Veldtman *et al.*, 2010). We compared D_{ij} values at each scale between the two species using a Wilcoxon Signed Rank Test (Hollander & Wolfe, 1999).

4.3 Results

Occupancy levels varied markedly between cells (**Fig. 4.2**). Despite this, there was a consistent relationship across all assessed QDGC containing invasive populations with high D_{ij} scores at the finest and coarsest scales [(i.e. plot (0.0025-0.025km) and regional (2.5-25km)] compared to the intermediate scales [(i.e. local (0.025-0.25km) and landscape (0.25-2.5km); see Table 4.1, **Fig. 4.3**)]. This suggests that at the very localized and broad levels the spatial distribution of *A. elata* in South Africa shows greater continuity than the relatively fragmented state of the distribution at the local and landscape scale.

The Friedmans Rank Sum Test (p<0.001) and one-way repeated measures ANOVA (p<0.001) indicated that there were differences in D_{ij} scores between scales. The post-hoc analysis showed that (a) populations at the plot scale were more contiguous than those at the both local and landscape scales (p<0.001); (b) local and landscape scales did not differ significantly; and (c) populations appear more contiguous at the regional scale than the landscape scale (p<0.01) but are not significantly different in structure to those at the plot and local scale.

Comparisons between the spatial structures of *A. elata* and *A. longifolia* populations indicate that populations of the latter are either more contiguous (p<0.05) or of similar spatial structure (p>0.05) across all scales (**Fig. 4.3**). The most notable difference was the more contiguous structure of *A. longifolia* populations compared with relatively fragmented structure of *A. elata* populations between 125m and 5km (**Fig. 4.3**).

4.4 Discussion

Our results suggest that stands of *A. elata* are contiguous and relatively abundant within the cells that they occupy. Despite the D_{ij} values being lower than may be indicative of a very abundant population (>1; Kunin, 1998) this suggests that processes associated with *A. elata* invasions at the plot scale do not seem to be restricting reproduction and spread, supporting our first prediction that invasive *A. elata* stands tend to be dense (and are likely to be increasing in density). Our second hypothesis, that ornamental-type introductions would result in fragmented populations, is only supported at a landscape scale. At a regional scale *A. elata* distribution appears to be relatively contiguous.

Our results indicate that the spatial distribution at the coarsest scale was relatively highly clumped compared to those at the intermediate scale. We would argue that this is still the result of human dissemination with the ornamental *A. elata* being introduced more frequently to areas of high population density or along roads. At these zones, resultant invasive populations will group into defined foci along roadways and available land surrounding conurbations as opposed to being spread throughout the broader landscape resulting in clumped distributions of populations (Watkins *et al*., 2003; Foxcroft *et al*., 2008; Christen & Matlack, 2009).

The relatively low D_{ij} scores at the local and landscape scale when compared with the plot and regional scales suggest that spatial distribution is scattered between 250m and 2.5km. Two possible causes are the fragmentation of available land at this scale resulting from the human habitats into which ornamental plants are placed and the lack of regional dispersal at these distances (Minor *et al*., 2009). These two limitations may be directly linked with natural dispersal being unable to drive expansion of populations beyond the local scale as roads, properties, and intensive management of human-dominated areas create

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fragmented landscapes with large distances between patches of suitable habitat (**Fig. 4.4**; Minor *et al.*, 2009). In such cases, secondary dispersal will be required either in the form of a natural mutualism such as birds and water or through movement of propagules by humans over these distances (Minor *et al.*, 2009). As *A. elata* is not adapted for dispersal by birds (O'Dowd & Gill, 1986) these medium-distance movements of propagules will rely heavily on human transportation and with deliberate introductions limited to personal preference, plantings of long-lived trees into gardens is likely to be infrequent resulting in low numbers of deliberately moved propagules over medium to long distances. Thus the most likely movement of seeds will be through unintentional human movement. Support for this notion is provided by the relatively continuous spatial structure at landscape scales of two sites where forestry is the dominant land use type (Storms River and Elgin sites). Heavy machinery used in silvicultural operations has been shown to be a key dispersal vector for many invasive species (Watkins *et al.*, 2003; Christen & Matlack, 2009), including other *Acacia* species (Kaplan *et al.*, in press).

If populations are dispersal limited, then we would predict that the scale-area curves would appear steep and the gradient only become shallow when dispersal barriers are overcome as the invasion progresses (with increased residence time), and so D_{ij} scores would become more consistent across spatial scales. Species with a longer residence time, larger initial propagule pressure, or extent of initial distribution would likely have scale-area curves more indicative of observed population dynamics. This seems to be the case for *Acacia longifolia* for which occupied cells were consistently contiguous across all scales assessed (**Fig. 4.3**). Furthermore, the most heavily occupied *A. elata* cells assessed in this study had steeper scale-area curves than for the most occupied *A. longifolia* cells, indicating that *A. elata* populations are not (yet) as dense as *A. longifolia* at landscape and fine scales. A more

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definitive test of these assumptions would be to assess species with similar human introduction pathways but different natural dispersal mechanisms. Research analysing the spatial structure of bird-dispersed species such as *A. cyclops* may provide more definitive comparisons regarding the influence of human use on the spatial structure of invasive plants. Alternatively, patterns in QDGCs that differ in known aspects of introduction effort could be compared, though data (e.g. date of introduction, and maps of plantings) are often not available for ornamental species.
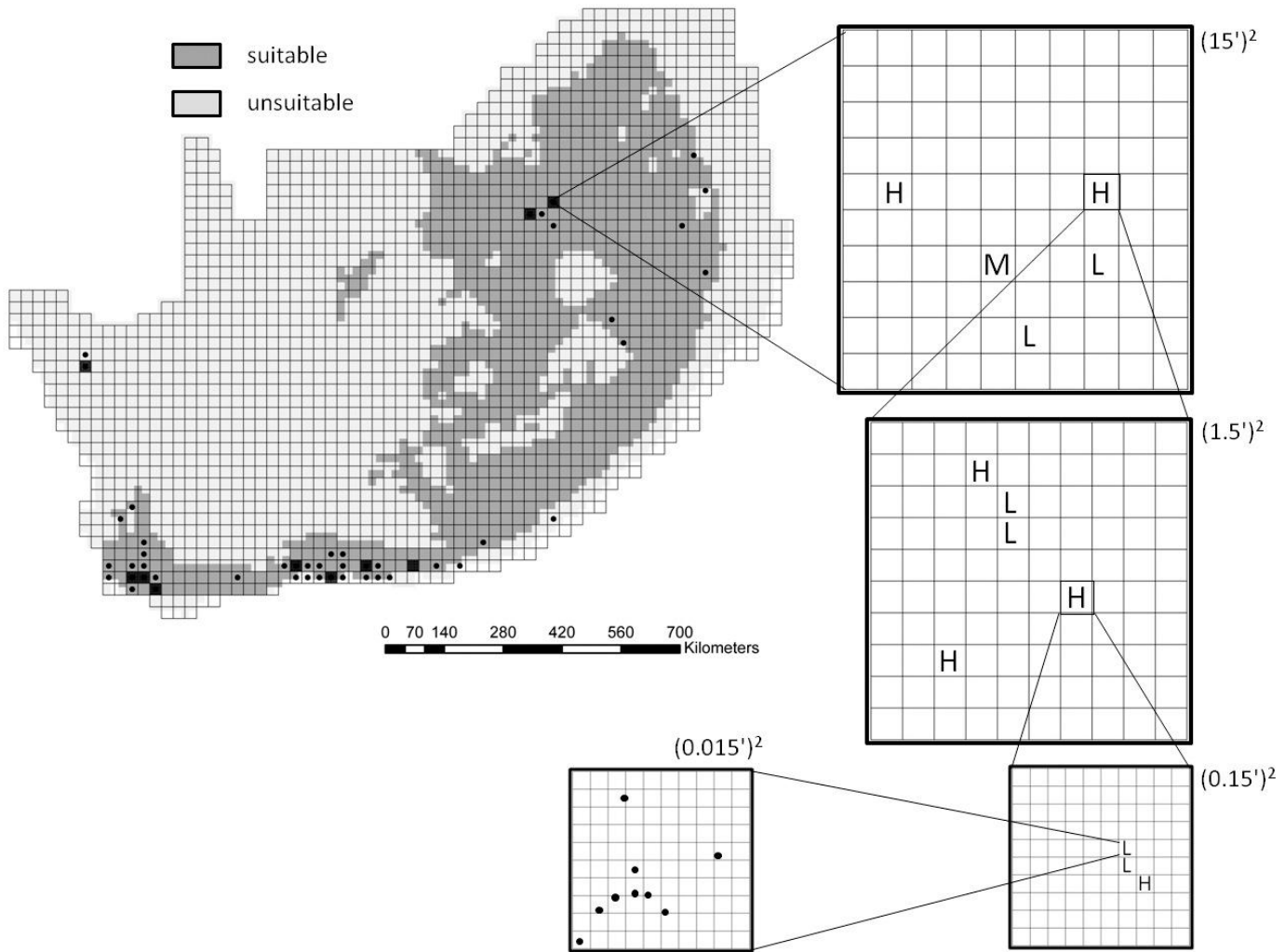
In summary, we believe that scale-area curves can provide useful insights for invasive species management, but only if the introduction dynamics are known (and specifically the relative roles of natural and human-mediated dispersal at different spatial scales).
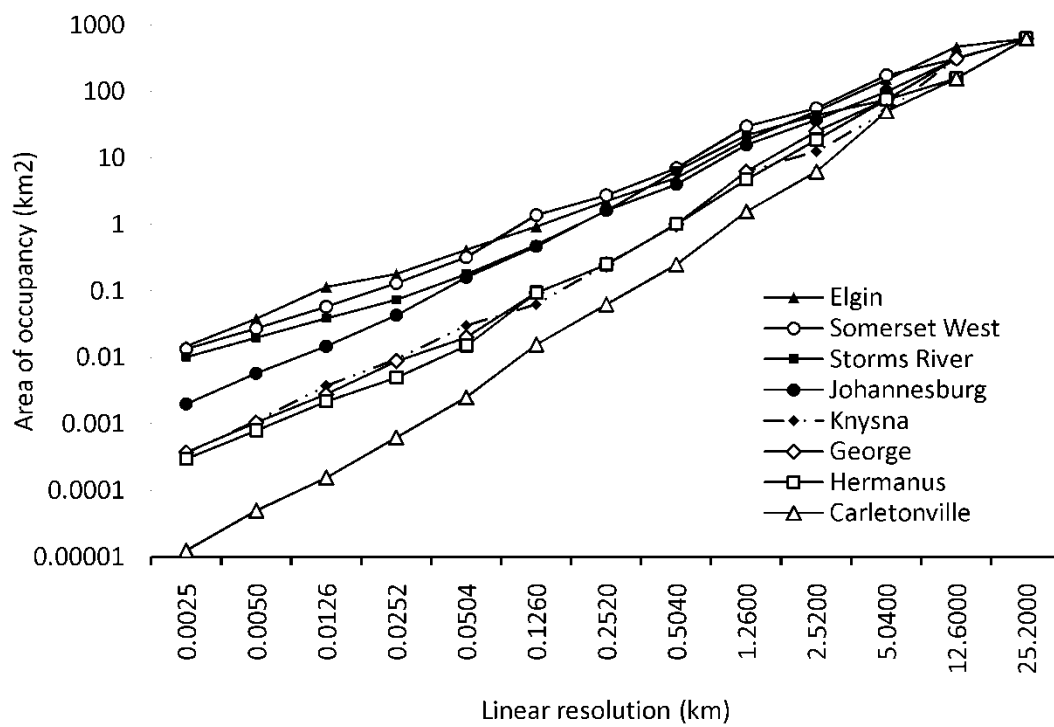
Acknowledgements

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Table 4.1 Scale-specific box-counting fractal dimensions (*Dij*) for quarter-degree grids cells occupied by *Acacia elata* in South Africa (linear resolution from 25 km to 2.5 m). D_{ij} explains the spatial makeup of a species between scales *i-j*; the maximum value of 2 indicates that coarse cells are completely filled with occupied small-scale cells, while a minimum value of 0 indicates the occupancy of a coarse-scale cell by a single occupied smaller scale cell.

QDGC	Latitude	Longitude	Scale (i-j)			
			2.5-25m	25-250m	250m-2.5km	2.5km-25km
			plot	local	landscape	regional
Elgin	-34° 15' S	19°00'E	0.92	0.88	0.66	0.92
Somerset West	-34° 15' S	18°45'E	1.00	0.70	0.71	0.91
Hermanus	-34° 30' S	19°15'E	0.76	0.33	0.10	0.40
Knysna	-34° 15' S	23°00'E	0.58	0.51	0.33	0.33
Storms River	-34° 00' S	23°45'E	1.13	0.63	0.55	0.88
George	-34° 00' S	23°15'E	0.60	0.57	0.00	0.62
Carletonville	-26° 30' S	27°15'E	0.23	0.00	0.00	0.25
Johannesburg	-26° 15' S	27°45'E	0.64	0.38	0.65	0.78

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Fig. 4.1 Quarter-degree grid cells occupied by *Acacia elata* (black dots) in South Africa. Dark grey and light grey shading indicates "suitable" and "unsuitable" habitat for *A. elata* based on bioclimatic modelling using invasive distribution records (Appendix S1). Cells sampled in this study are shaded completely black (8 suitable and 2 unsuitable). An example of the fractal sampling design used to determine occupancy at four different scales is indicated on the right with one low and one high occupancy cell selected at each resolution where possible: Coarse (15' latitude by 15'longitude), landscape (1.5' by 1.5'), local (0.15' by 0. 15') and plot (0.015' by 0.015').

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Fig. 4.2 Scale–area curves for *Acacia elata* for quarter-degree grid cells surveyed at multiple scales in South Africa. Steeper slopes indicate fragmented populations, whereas gradual gradients are typical of more contiguous populations.

Fig. 4.3 Comparison between mean *Acacia elata* (*n* = 9; this study) and *Acacia longifolia* (n=12; Veldtman et al. 2010) box counting fractal dimensions (D_{ij}) for quarter-degree grid cells surveyed at multiple scales in South Africa. Maximum values of 2 indicate that coarse cells are completely filled with occupied fine scale cells; a minimum value of 0 indicates the occupancy of a coarse scale cell by a single occupied fine-scale cell (Wilcoxon signed rank test, p<0.05*, p<0.01**).

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Fig. 4.4 Position of invasive *Acacia elata* trees spreading in a suburban area of Knysna, Western Cape, South Africa.

Chapter 5: Thesis conclusions

5.1 Invasive Australian acacias in South Africa: a model study group

Australian acacias have a long history of introduction and naturalization/invasions globally (Richardson *et al.*, 2011). In South Africa the costs of dealing with Australian acacia invasions have amounted to billions of Rand (Van Wilgen *et al.*, 2012). To date species with broad invasive distributions in South Africa associated with forestry and dune stabilization introductions have received the majority of attention in literature (reviews in Gibson *et al.*, 2011; Van Wilgen *et al.*, 2011; Wilson *et al.*, 2011). However, there is a growing realization that species which currently occupy small portions of their potential range represent a growing future invasion threat that can be termed "invasion debt" (Essl *et al.*, 2011). In terms of Australian acacias in South Africa, the majority of species were introduced for use as ornamental plants. Developing an understanding of why species introduced for ornamental horticulture have not invaded to the same extent as similar commercial forestry species and dune stabilization formed the basis of my thesis.

To explore the relationship between the ornamental trade and invasive spread I focused on *Acacia elata* invasions in South Africa. This species provided the ideal model species for studying ornamental invasive trees due to its well-documented introduction history (Poynton, 2009), limited current but broad potential distribution (Mgidi *et al.*, 2007), and the need for a management plan. Furthermore, the past use of Australian acacias as a model group for the study of invasive trees (Richardson *et al.*, 2011) and the existence of a framework for their invasion management (van Wilgen *et al.*, 2011) afforded me the opportunity to explore general questions surrounding the influence of human pathways of

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introduction on invasive success while using my findings to development a clear national-scale strategic approach for *A. elata*.

5.2 Conclusion 1 – The ornamental species *Acacia elata* is not limited by reproductive traits

I initially looked at determinants of invasions at different stages along the introduction-naturalization-invasion continuum by assessing the reproductive capabilities of *A. elata* in South Africa and comparing them to more widely distributed *Acacia* species (**Chapter 2**). I showed that intrinsic species traits linked to reproductive biology of *Acacia* species do not appear to be limiting the spread of ornamental trees in South Africa as *A. elata* stands were able to produce large amounts of viable seed annually which over time develop substantial seedbanks. Despite this we did find that *A. elata* appears to lack a secondary dispersal agent that would act at any significant scale, unlike *A. cyclops* which is effectively dispersed by birds (Glyphis *et al.*, 1981). This suggests that for any secondary dispersal at the regional scale the species would be heavily reliant on human movement. Due to agreements in place that restrict trade in ornamental Australian acacias this is unlikely to occur deliberately. Most secondary dispersal will be via accidental human movement or along water courses.

5.3 Conclusion 2 - Limitations to the distribution of ornamental species is more closely linked to planting history and human movement than to intrinsic species traits

Human uses and the resultant pathway of introduction have a substantial effect on introduction conditions such as propagule pressure, introduction foci and recipient environment, which have all been shown to impact invasive success (Wilson *et al.*, 2009). I therefore analysed the relative influence of human dictated introduction conditions compared to intrinsic species traits on a species ability to overcome barriers to dispersal and spread (**Chapter 3**). I showed that at least in the initial stages of invasions the introduction

conditions of a species have a greater influence on species spread and abundance than intrinsic species traits. Results also indicated that introduction conditions typical of ornamental plantings - such as low propagule pressure, placement in random climatic space, reduced long-distance dissemination, by humans, and placement of foci in suburban/urban fragmented landscapes - limited both the population size and spread of ornamental trees. Thus it appears that rather than intrinsic species traits limiting the current distribution of ornamental *Acacia* species in South Africa this is likely to be the result of planting history. This raises concerns related to the future of these invasions as the longer species are present, the more opportunities for overcoming barriers will be afforded them. These species therefore represent a substantial future invasion risk with three ornamental Australian acacia species indicating substantial potential invasive distributions in the country (**Fig. S3.6**).

5.4 Conclusion 3 - Aspects of the introduction history and species-specific traits of an invasive species are discernible in the structure of invasive populations at multiple scales

Ultimately, this study shows that *A. elata* has the potential to become a major invasive species in South Africa but that it has until now been limited by a combination of factors associated with its introduction history and limited dissemination. With these limitations set to decrease with time resulting in further spread, management needs to be implemented that focuses on: (a) the removal of new populations; (b) the containment of larger populations through restricting regional movement of propagules; and (c) limiting new invasion foci by reducing seed set of garden plants acting as potential sources of spread.

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In **Chapter 3** I explored how the aforementioned processes associated with human introduction and reproductive capabilities have shaped the spatial structure of *Acacia elata* populations over a range of spatial scales (**Chapter 4**). I showed that introduction history left clear artefacts ("signatures") in population structure and observed three definitive scale-associated patterns that I then linked to processes observed in **Chapter 1** and **2**. These were: (a) at the plot scale, processes related to natural reproduction are promoting spread; (b) fragmented plantings related to haphazard ornamental plantings and limited secondary human and natural dispersal are slowing local and landscape level spread, resulting in fragmented populations at the landscape level; and (c) the introduction of ornamental trees around conurbations and roadways result in defined introduction foci at the landscape scale. This work showed that the combination of limited secondary dispersal observed in the reproduction dynamics of *A. elata* in combination with haphazard plantings at the broader scale linked to its human use appears to be what is currently limiting the species invasive distribution.

5.5 Management recommendations

Acacia elata currently has a broad national distribution making national-scale eradication unrealistic (Mgidi *et al.*, 2011). The species is presently only used as an ornamental species and has little to offer as a commercial crop due to its low wood quality and less desirable properties for tannin compared to other acacias (Poynton, 2009). This places the species in South Africa firmly within the category of "widespread invader with few benefits" with the resultant strategic goal to "measurably reduce impacts to a sustainable and tolerable level" (Van Wilgen *et al.*, 2011). A range of management practices will need to be carried out at different scales to achieve this aim.

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Chapter 2 of my thesis indicated that at the local-scale eradication is possible when invasions are recent or when populations have experienced disturbance in the recent past as seedbanks are still manageable. In such cases, mechanical clearing is suggested as plants do not resprout. Post-clearing follow-up operations within four years are needed to prevent secondary seeding by plants emerging from the seedbank. In cases where seedbanks need to be stimulated, fire is likely to provide the best results.

In established stands, seedbanks of *A. elata* (like those of all invasive acacias; Richardson & Kluge, 2008) represent a significant obstacle to management. These populations should become candidates for containment. Further dispersal of seeds by humans and through dispersal along rivers represents the greatest threats for further spread. Consequently, options for reducing the likelihood of movement of seed-containing soil through human activities such as road building should be examined in zones identified as high-risk areas for further spread. The demographic placement of ornamental trees in large gardens and green belts could provide a valuable platform for educating the public as people in these areas may already have a greater interest for flora and biodiversity issues and thus be more concerned with potential threats.

The most effective way of preventing substantial future spread of this species would be to limit secondary dispersal over regional scales (**Chapter 4**). Deliberate secondary dispersal of *A. elata* has also been substantially reduced though the agreement between Working for Water (section of the Department of Environmental Affairs; the agency responsible for managing invasive alien plants nationally) and the South African Nurserymen's Association to stop the commercial trade of plant species known to be invasive, including species of Australian acacias (details in Richardson *et al*., 2011b). It is likely that the current limited

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dispersal of *A. elata* and other ornamental acacias can be attributed to some degree to these restrictions and it is suggested that these regulations should be continued and that enforcement measures should be improved.

I found that the most heavily invaded areas occur in or near pine plantations. From my experience in the field I would highly recommend the development of strong relations between invasion managers and forestry managers as forestry activities seem to represent the clearest vector of spread for *A. elata* and potentially other ornamental species at the regional scale between urban/suburban settings and natural/open landscapes as was shown in **Chapter 4**. In this respect, *A. elata* is very similar to another emerging invasive acacia, e.g. *A. stricta* (Kaplan, 2012). This is due to the combination of long gaps between planting of forestry crops and harvest when stands are left for long periods without management and the frequent movement of heavy machinery along gravel roads that act as dispersal agent for seeds (Watkins *et al.*, 2003). These areas will be the greatest concern in containment efforts and if left unmanaged due to poor relations could result in populations overcoming barriers at the regional scale (**Chapter 4**) with these types of dispersal shown to increase rate of spread (**Chapter 3**). Conversely, strong relationships with forestry companies could cement a powerful alliance when attempting management of populations, as isolated pockets of *A. elata* among plantations represents an easy target for removal by forestry companies trying to improve their environmental image.

The combined findings of **Chapter 2** and **Chapter 4** suggest that there are still numerous planted trees within gardens, representing a significant source of propagules with the potential to drive future invasions. Complications related to mechanical removal of these trees may exist due to conflicts of interest with land owners. Biological control would be

useful to restrict current invasions and reduce the risk of future invasions without generating conflict with landowners (Zimmerman *et al*., 2004). Whether this is a feasible route to follow will require further exploration, but contiguous landscape-level foci (**Chapter 4**) and ease of access to large trees within or in close proximity to conurbations could reduce dispersal restrictions associated with other biological control agents (Van Wilgen *et al*., 2004).

Although this study focused on a single species and genus, the findings improve our understanding of the influence of human use on the invasion trajectory of invasive species in general, something that clearly requires consideration when assessing the invasion risk of a potential candidate for introduction.

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Supporting Information

Fig. S2.1 Seed rain density (seeds.m^{-2}) at different distances from the terminal branches (0m)

of *Acacia elata* canopies (error bars represent 95% CI).

Fig. S2.2 Relationship between seed rain and tree height of twenty five *Acacia elata* trees growing in the Western Cape, South Africa, indicating an increase in seed production with greater height

Fig. S2.3 Log mean seed density of seedbanks found underneath *Acacia elata* stands at the four different depths analysed for the Warwick farm and Spanish farm sites (error bars represent 95% confidence intervals)

100
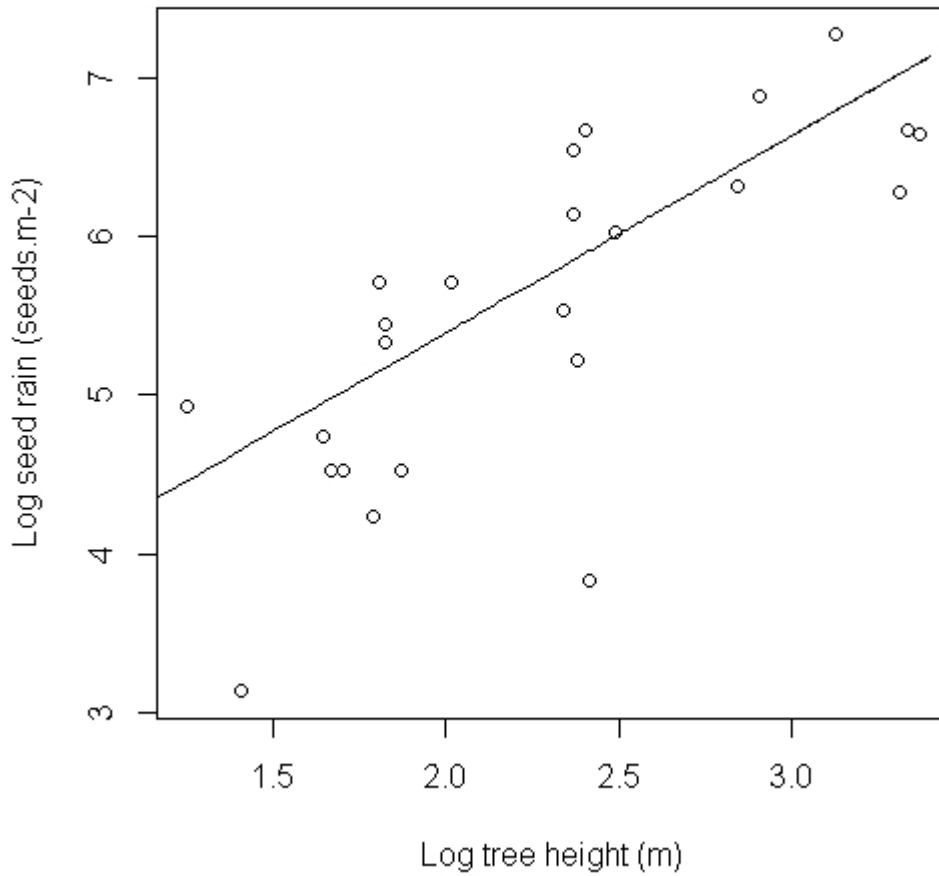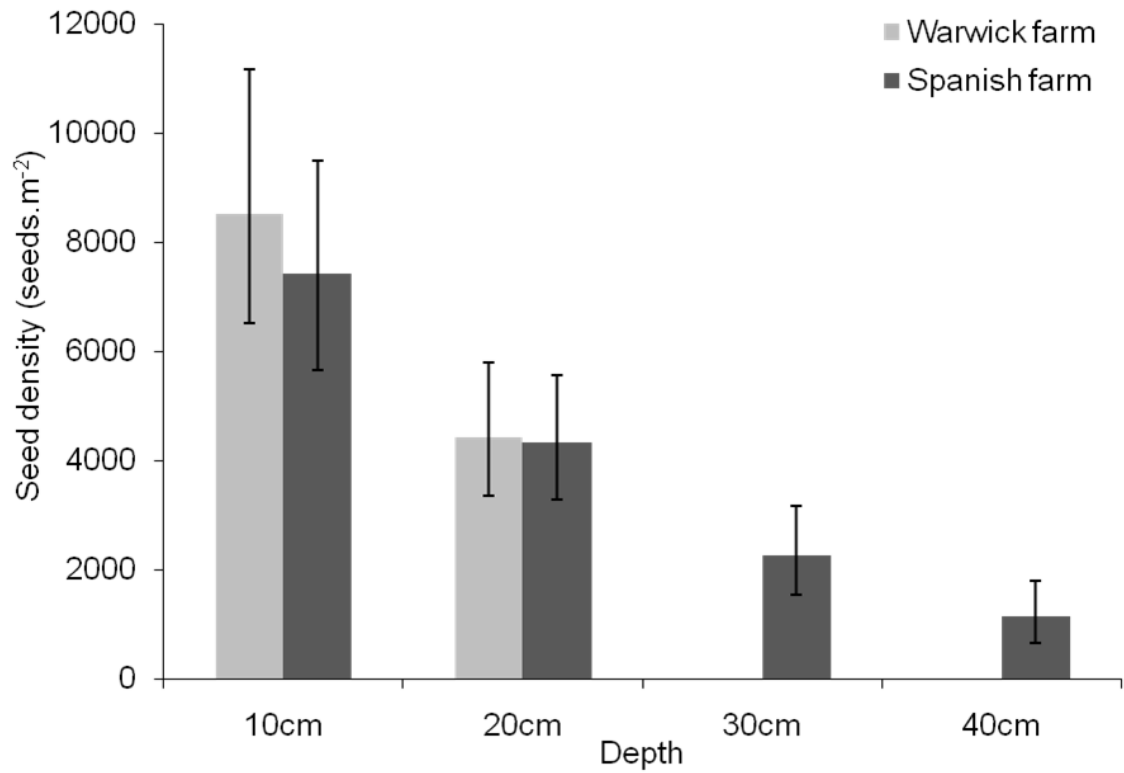
Table S3.1 Summary of data sources, cleaning and final data points used in distribution modelling of invasive acacia species in South Africa

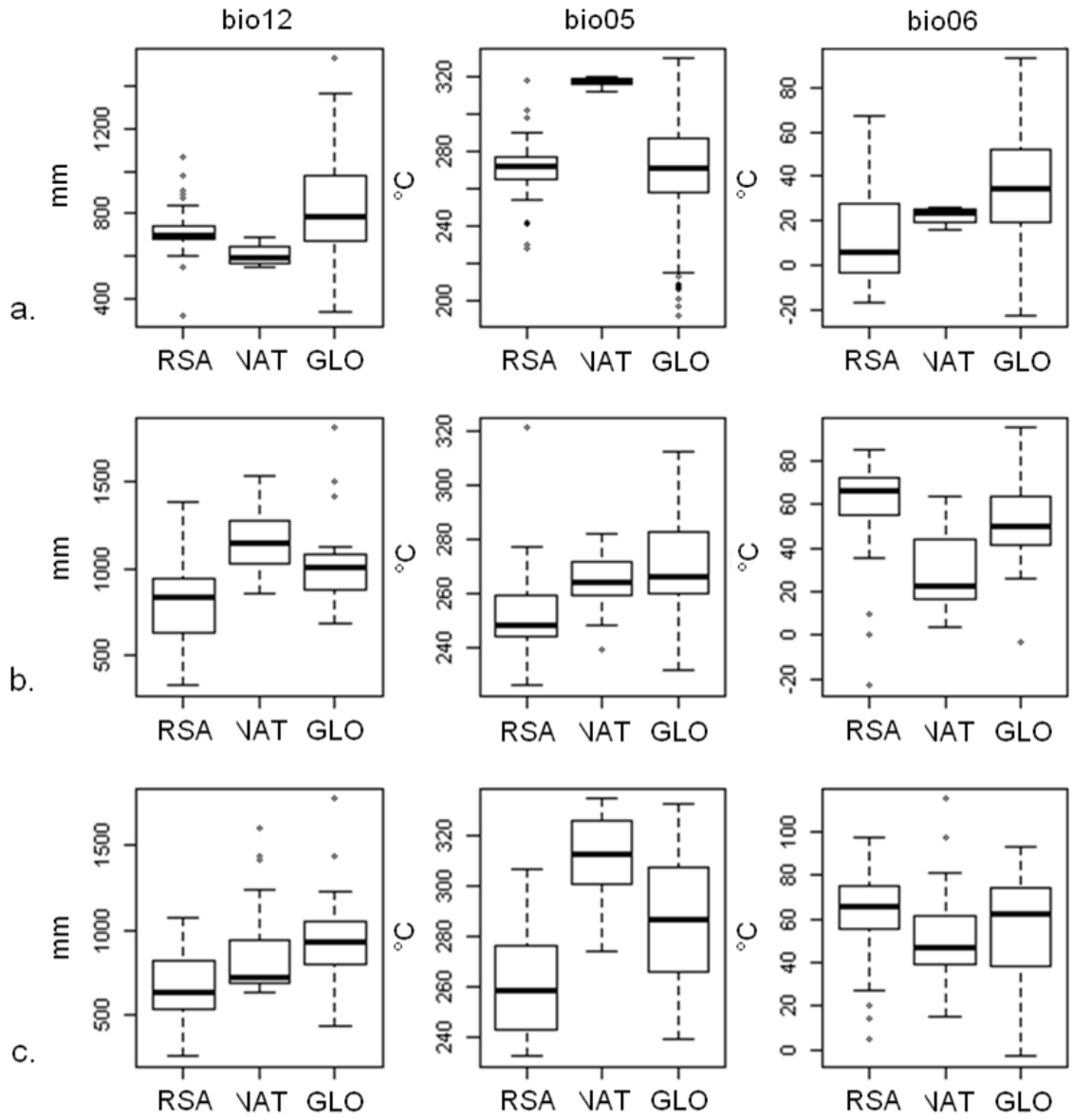| Data set	Type	*A. baileyana*	*A. cyclops*	*A. dealbata*	*A. decurrens*	*A. elata*	*A. longifolia*	*A. mearnsii*	*A. melanoxylon*	*A. podalyriifolia*	*A. pycnantha*	*A. saligna*
All	Raw	1050	2146	12269	1904	1086	8060	5151	13610	1108	8095	3875
	Clean	288	1022	8923	510	247	1381	1982	8303	201	1640	328
	Regularized	160	409	636	243	88	348	659	669	145	620	314
NAT	Regularized	9	103	333	74	44	272	173	503	64	497	28
RSA	Regularized	38	234	289	127	28	47	448	124	45	59	64
GLO	Regularized	113	72	14	42	16	29	38	42	36	64	222

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Fig. S3.1 Variation from recent historical climatic conditions (1975H) for the three Bioclim variables used in models calibrated with South African distribution records (RSA), native distribution records (NAT) and invasive distribution records for all countries excluding South Africa (GLO). Data points correspond to distribution records from the relevant region falling within 10' grid cells for the four forestry species *A. dealbata* (a), *A. decurrens* (b); *A. mearnsii* (c) and *A. melanoxylon* (d). The three variables were annual precipitation (Bio12), maximum temperature of the warmest month (Bio05), and minimum temperature of the coldest (Bio06).
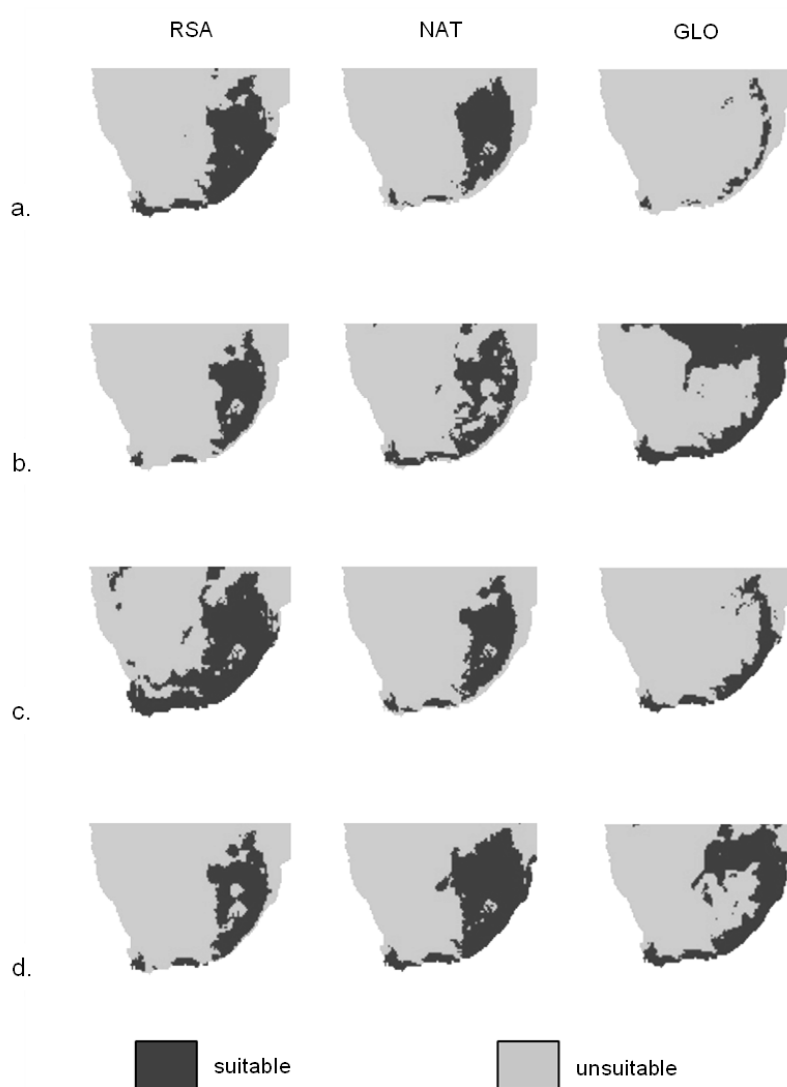
Fig. S3.2 Variation from recent historical climatic conditions (1975H) for the three Bioclim variables used in models calibrated with South African distribution records (RSA), native distribution records (NAT) and invasive distribution records for all countries excluding South Africa (GLO). Data points correspond to distribution records from the relevant region falling within 10' grid cells for the four dune species *A. cyclops* (a), *A. longifolia* (b); *A. pycnantha* (c) and *A. saligna* (d). The three variables were annual precipitation (Bio12), maximum temperature of the warmest month (Bio05), and minimum temperature of the coldest (Bio06).

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Fig. S3.3 Variation from recent historical climatic conditions (1975H) for the three Bioclim variables used in models calibrated with South African distribution records (RSA), native distribution records (NAT) and invasive distribution records for all countries excluding South Africa (GLO). Data points correspond to distribution records from the relevant region falling within 10' grid cells for the three ornamental species *A. baileyana* (a), *A. elata* (b); and *A. podalyriifolia* (c). The three variables were annual precipitation (Bio12), maximum temperature of the warmest month (Bio05), and minimum temperature of the coldest (Bio06).
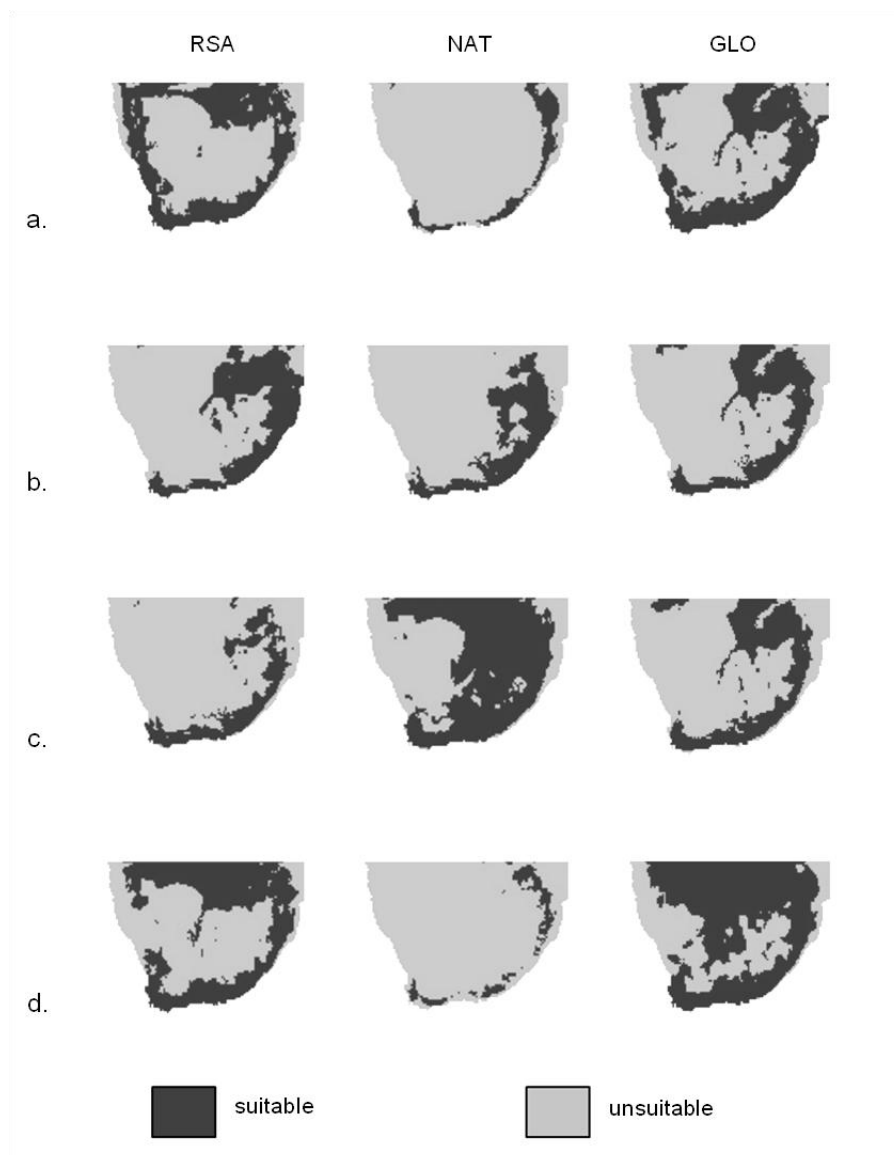
Fig. S3.4 Projected bioclimatic niches predicted by correlative distribution models for each of the four forestry species *A. dealbata* (a), *A. decurrens* (b); *A. mearnsii* (c) and *A. melanoxylon* (d) in South Africa. Models were calibrated using South African distribution records (RSA), native distribution records (NAT) and invasive distribution records for all countries excluding South Africa (GLO) for each species.
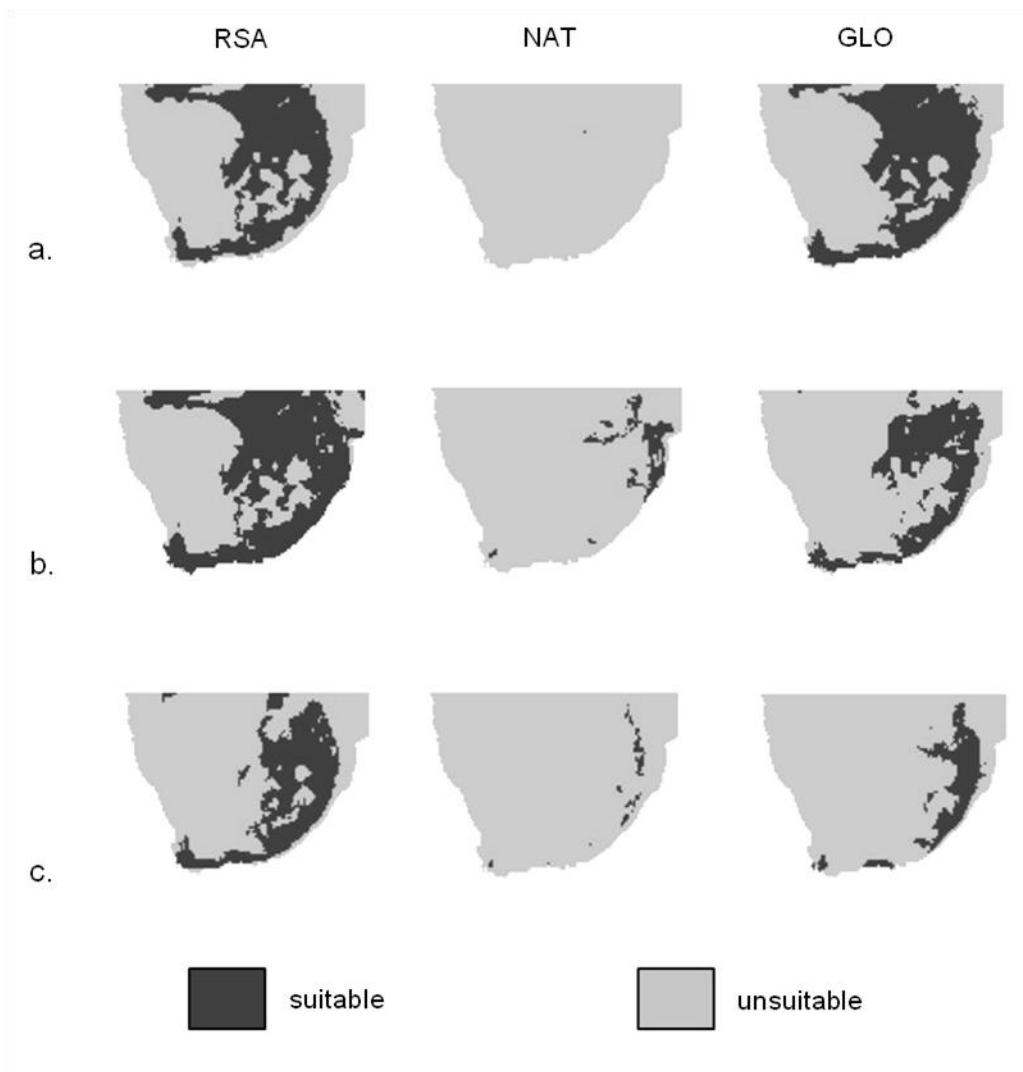

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Fig. S3.5 Projected bioclimatic niches predicted by correlative distribution models for each of the four dune species *A. cyclops* (a), *A. longifolia* (b); *A. pycnantha* (c) and *A. saligna* (d) in South Africa. Models were calibrated using South African distribution records (RSA), native distribution records (NAT) and invasive distribution records for all countries excluding South Africa (GLO) for each species.

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Fig. S3.6 Projected bioclimatic niches predicted by correlative distribution models for each of the three ornamental species *A. baileyana* (a), *A. elata* (b); and *A. podalyriifolia* (c) in South Africa. Models were calibrated using South African distribution records (RSA), native distribution records (NAT) and invasive distribution records for all countries excluding South Africa (GLO) for each species.

Appendix S3.1

A species distribution model was created in order to serve as a background for a dynamic lattice model based on basic growth and dispersal processes. *Acacia longifolia* data was selected for use when calibrating the model due to the accuracy of South African distribution records and availability of data on life history traits and abundance (Milton & Hall, 1981; Veldtman *et al.*, 2010; Marchante *et al.*, 2011). We first combined all distribution records (i.e. NAT+RSA+GLO) in the SDM to try and cover the full range of climate space occupied by *A. longifolia*, based on the same climatic variables as above. Specifically, the SDM was trained in MAXENT v. 3.3.3k (Phillips *et al.*, 2006) using the same WorldClim 10' resolution gridded bioclimatic raster set before being projected to the WorldClim Version 1.4 (Release 3) 30'' resolution gridded bioclimatic raster set (Hijmans *et al.*, 2005; www.worldclim.org; accessed 01.08.2012) for the Western Cape. To ensure that pseudo absence data were selected from relevant regions, 10 000 background points were selected from Köppen-Geiger climate zones containing presence points (Köppen 1936; Phillips & Dudík, 2008; following Webber *et al.*, 2011). All settings were left as default: 'logistic output', 'create response curves', 'jacknife measures of variable importance', 'do clamping' and a regularization value of 1; however, as recommended for invasive species, only hinge features were used to build the model (Elith *et al.*, 2010). The globally trained model was then projected to the Western Cape.

To reduce the chances of over fitting and to limit omission errors, the model projection was assessed by using the lowest presence threshold (LPT; Pearson *et al.*, 2007) to define whether a cell was projected to be a 'presence' or 'absence' (**Fig. S3.7**). As is suggested for analysis of projections made for invasive species (Webber *et al.*, 2011; Thompson *et al.*,
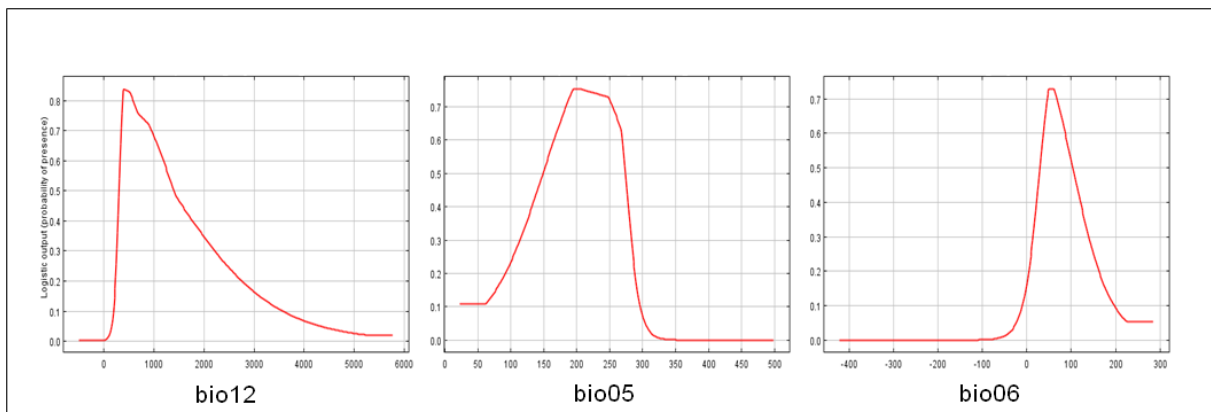
111

2011), the binary presence-absence map was used to calculate sensitivity (proportion of known presences predicted present) and prevalence (proportion of available area predicted present), which was tested for significance with an exact one-tailed binomial test (Pearson *et al*., 2006; Thompson *et al*., 2011).

The model projected to the Western Cape was statistically significant (P<0.001) according to the exact one-tailed binomial test. The model showed full sensitivity in the projected range (1) with a reasonably high prevalence of 0.297, and a LPT of 0.23. While prevalence was high, commission errors were considered more reasonable than omission errors for modelling invasive species and thus accepted (Araújo & Peterson, 2012). Finally, response curves indicated nothing to suggest the model projections to the novel range were unreasonable (**Fig. S3.8** and **S3.9**).
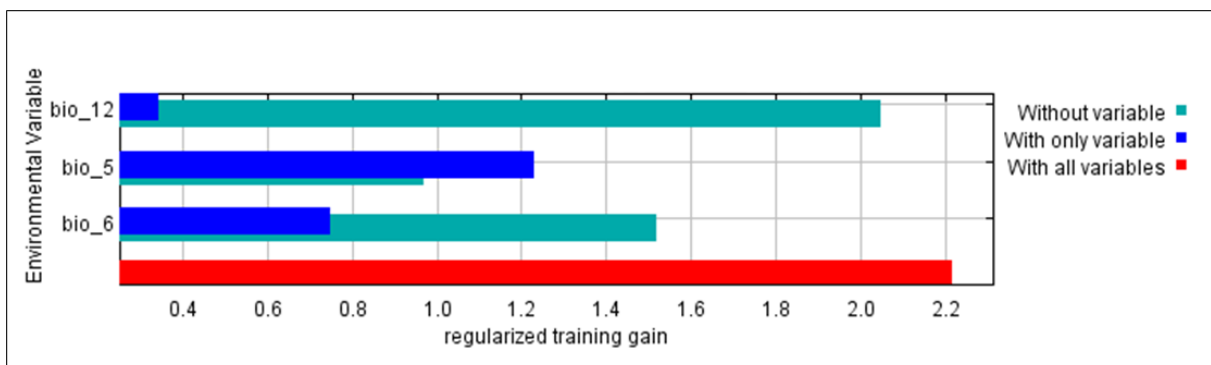
Fig. S3.7 Relative habitat suitability identified by correlative distribution modelling for *Acacia longifolia* in the Western Cape, South Africa. Red represents cells projected as climatically suitable, using the lowest presence threshold (LPT) as the binary threshold. Models were trained using all available distribution data globally and pseudo-absence data drawn from Köppen-Geiger climate zones containing presence points.

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Fig. S3.8 Bioclimatic response curves generated by MAXENT models trained on global distribution data range for *Acacia longifolia*, and projected to the Western Cape, South Africa. Bioclimatic variables used: maximum temperature (bio05), minimum temperature (bio06), and annual rainfall total (bio12)

Fig. S3.9 Bioclimatic variable testing gains (x-axis) with and without each variable, for MAXENT models projected to the Western Cape, South Africa. Bioclimatic variables represented are: maximum temperature (bio05), minimum temperature (bio06), and annual rainfall total (bio12).

Table S3.2 Explanations and relevant references used to calculate three different reproductive rates (*r*) used for populations in the cellular automaton simulations.

Limitation	Mean seeds per tree	Max seeds per tree	Min seeds per tree	References
Annual seed production estimates for trees in the Western Cape	28750	48000	9500	Milton & Hall, 1981; Dennill, 1985
Seed predation (45%)	15812	26400	5225	Holmes, 1990
Viable seed (90%)	14231	23760	4703	Milton & Hall, 1981; Marchante *et al*., 2011
Spontaneously germinating	285	475	94	Milton & Hall, 1981; Marchante *et al*., 2011
Falling outside of parent canopy (0.5%)	43	71	14	Milton & Hall, 1981; Marchante *et al*., 2011
Estimated seedling survival in open, unburnt Fynbos (0.5%)	0.2	0.4	0.1	Hoffmann & Impson, unpublished
Estimated number o seedlings produced over three year period (*r*)	0.5	1.2	0.2	