Ailanthus altissima: an assessment of its distribution at different spatial scales and options for management in South Africa

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Declaration

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ABSTRACT

The constant flow of goods into and out of cities has resulted in the proliferation of invasive species in urban areas and, because of this, cities are viewed as 'hotspots' for invasive species. The rise of global trade and long distance transportation will ensure that further introductions will take place in urban ecosystems. Conditions that have been altered due to human activities enable some alien species to proliferate rapidly throughout urban centres, often also spreading into natural and semi-natural areas at the urban/wildland interface. Evaluating the current distribution of an invader by analysing potential patterns in its distribution, as well as determining the potential distribution of a species over multiple landscapes and identifying factors that promote its spread, is essential for determining the full extent of an invader. Understanding 1) where a species is; 2) where a species may spread to; and 3) the factors that promote the spread of a species are all needed to gain an understanding of the biological and biogeographical preferences that facilitate the spread of the species. This is best achieved by using a multi-scale analysis that studies all aspects of an invasive species over a variety of spatial scales. This study focusses on a notorious northern hemisphere invader - *Ailanthus altissima* – that, although having been introduced into South Africa in 1834, is yet to replicate similar levels of invasion success. I adopted for a multi-scale analysis of the species evaluating the current and potential distribution of the species at a global scale (Chapter 1), national scale (Chapter 2) and local scale (Chapter 3). Each chapter addresses a central aim in which a number of research questions are evaluated.

In Chapter 1 I assess the biogeography, distribution, and habitat suitability of *A. altissima* by evaluating the current and potential distribution of the species (based on climatic suitability) at both a global scale and a national scale (in South Africa). The main conclusions of this chapter are that 1) online databases (although outdated at times) provide an accurate representation of the distribution of invasive species and should therefore be accessed. This was ascertained by cross referencing a number of online databases to evaluate whether they were largely in agreement with one another in terms of the distribution of an invader; and 2) modelling the potential distribution of an invasive species based on climatic suitability serves as a good first approximation of potential species spread. Although this may be true, it was also suggested in this chapter that to accurately quantify the potential distribution of an invasive species, other distribution drivers (such as land use and human

mediated disturbances) need to be incorporated into the design of a species distribution model.

Chapter 2 evaluates the degree of range filling exhibited by *A. altissima* in South Africa and identifies areas at risk of future invasion. This chapter also identifies specific factors that promote the spread of the species at a global and national scale. I determined that at the global scale, climate had the highest influence on the distribution of *A. altissima* whereas at the national scale, human mediated disturbances exerted a higher influence on the distribution of the species. This chapter builds on the concepts proposed in Chapter 1 by highlighting the importance of incorporating different environmental variables at various spatial scales to identify potential invasion 'hotspots'. I conclude that the multi-scale approach presented in this chapter enables the early detection of invasive species, preventing damage associate with their potential spread. Also, the novelty of this approach is particularly effective when it comes to analysing urban invaders.

The third chapter evaluates the distribution pattern of *A. altissima* within the City of Cape Town by using the suburb of Newlands as a case study. In addition, it determines potential options for management at a city scale. It can be concluded that fine-scale analysis of invasive species distributions is best achieved using Geographic Information System (GIS) techniques and that such these ultimately help to identify potential areas susceptible to future invasion while delimiting unsuitable areas. I determined that *A. altissima* has a preference for affluent urban areas with podzolic soils that are exposed to high levels of rainfall within the City of Cape Town. Using this information, I determined that there is a large capacity for further spread by the species throughout the city. The systematic approach that we used in Newlands is an effective way of gauging the full extent of an invader and is especially effective for evaluating the population structure of a particular invasive species. Future studies should adopt this approach in conjunction with remote sensing techniques to achieve the best possible results.

The final chapter of this thesis provides the overall conclusions in which all the main findings are highlighted.

Altogether, the approach presented in this thesis is an effective method that could be used on other emerging, urban invaders globally. The systematic, multi-scale analysis proposed in this project showed high levels of success and it is my belief that this project achieved its desired aims.

OPSOMMING

Die voordurende vloei van goedere in en uit stede het tot gevolg dat indringerspesies vinnige in stedelike gebiede versprei, en stede dus as “brandpunte” vir indringerspesies beskou word. Die toename in internasionale handel en langafstand vervoer dra verder by tot die verspreiding van nuwe indringerspesies in stedelike gebiede. Omgewingstoestande wat verander het weens menslike aktiwiteite, stel sommige uitheemse spesies in staat om vinnig te floreer in stedelike sentrums. Dit stel hierdie spesies ook dikwels in staat om te versprei na omliggende natuurlike en semi-natuurlike gebiede. Om die volle omvang van ʼn indringer te bepaal is dit belangrik om die huidige verspreidingspatrone van die indringer, sy potensiële toekomstige verspreiding oor ekosisteme, asook na die faktore wat sy verspreiding kan bevorder, in ag te neem. Om die biologiese en biogeografiese voorkeure wat ʼn spesie se verspreiding sal fasiliteer te verstaan, moet daar begrip verkry word vir 1) waar ʼn spesie is; 2) waarheen ʼn spesie kan versprei; en 3) die faktore wat sy verspreiding kan bevorder. Dit word bepaal deur gebruik te maak van ʼn multi-skaal analise wat na alle aspekte van ʼn ndringerspesie oor verskeie ruimtelike skale bestudeer. Hierdie studie fokus op *Ailanthus altissima* wat ʼn aggressiewe indringer in die Noordelike halfrond is. Hoewel *A. altissima* reeds sedert 1834 in Suid-Afrika voorkom, het hierdie indringer nog nie dieselfde vlakke van indringing soos in die Noordelike halfrond, bereik nie. Ek het ʼn multi-skaal ontleding opgestel om die spesie se huidige en potensiële verspreiding op globale skaal (hoofstuk 1), nasionale skaal (hoofstuk 2) en plaaslike skaal (hoofstuk 3) te bepaal. Elke hoofstuk het ʼn sentrale doelstelling waarin ʼn aantal navorsingsvrae geëvalueer word.

In die eerste hoofstuk bepaal ek die biogeografie, verspreiding en habitatgeskiktheid van *A. altissima* deur die evaluering van die huidige en potensiële verspreiding van die spesie (gebaseer op klimaatstoestande geskiktheid) op beide 'n globale skaal en 'n nasionale skaal (Suid-Afrika). Die belangrikste gevolgtrekkings van hierdie hoofstuk is dat 1) aanlyn databasisse (hoewel verouderd by tye) verskaf 'n akkurate voorstelling van die verspreiding van indringerspesies en moet dus volgehou word. Dit was vasgestel deur kruisverwysings in 'n aantal van die aanlyn databasisse. Die databasisse is geëvalueer om te bepaal of hulle grootliks ooreenstem in terme van die verspreiding van indringerspesies; 2) en die modellering van die potensiële verspreiding volgens die geskiktheid van klimaatstoestande.

Om die potensiële verspreiding van 'n indringerspesies meer akkuraat te bepaal, is daar aanbeveel dat, ander verspreiding faktore soos grondgebruik en mensgemaakte versteurings, in die verspreidingsmodel ingebou moet word.

Hoofstuk 2 evalueer tot watter mate die gebiede wat deur die model voorgestel is reeds deur A. altissima beset is, en identifiseer gebiede wat die risiko van toekomstige indringing beloop. Hierdie hoofstuk identifiseer ook spesifieke faktore wat die verspreiding van hierdie spesie op 'n globale en nasionale skaal bevorder. Daar is vasgestel dat klimaat die grootse invloed op die spesie se verspreiding op ŉ globale skaal het. Op nasionale skaal het mensgemaakte versteurings ŉ groter invloed op die verspreiding van die spesie uitgeoefen. Hierdie hoofstuk bou voort op die konsepte in hoofstuk 1, deur klem te lê op die belangrikheid van die integrasie van verskillende omgewingsveranderlikes op verskeie ruimtelike skale om potensiële 'brandpunte' van indringing te identifiseer. Die multi-skaal benadering van hierdie hoofstuk stel ons in staat tot vroeë opsporing van indringerspesies wat sodoende gepaardgaande skade kan voorkom. Hierdie benadering is veral effektief in die ontleding van indringerspesies in stedelike gebiede.

Die derde hoofstuk evalueer die verspreidingspatroon van *A. altissima* binne die Stad Kaapstad deur die woonbuurt Nuweland as studiegebied. Dit bespreek ook die moontlike opsies vir bestuur op ŉ stedelike skaal. Daar kan tot die gevolg kom dat Geografiese Inligtingstelsel (GIS) tegnieke effektief aangewend kan word om fynskaalse ontleding van indringerspesies verspreiding te doen. Dit is effektief om gebiede wat vatbaar vir toekomstige indringing te identifiseer, terwyl ongeskikte gebiede geëlimineer kan word. Ek het vasgestel dat in die Stad Kaapstad, *A. altissima* gegoede stedelike gebiede met "podzolic" gronde verkies wat blootgestel word aan hoë vlakke van reënval. Hierdie inligting dui daarop dat daar ŉ hoë kapasiteit is vir verdere verspreiding van die spesie in die stad. Die sistematiese benadering wat in Nuweland gebruik is, is 'n doeltreffende manier om die volle omvang van 'n indringer te bepaal en is veral effektief vir die evaluering van die bevolking struktuur van 'n bepaalde indringerspesie. Toekomstige studies behoort hierdie benadering in samewerking met afstandswaarneming tegnieke toe pas vir die beste moontlike resultate.

Die laaste hoofstuk van hierdie tesis bied algehele gevolgtrekkings waarin al die belangrikste bevindings uitgelig word.

Alles in ag geneem, kan die benadering in hierdie tesis as 'n effektiewe metode toegepas word op ander opkomende, stedelike indringers wêreldwyd. Die sistematiese, multi-skaal analise wat voorgestel word in hierdie projek toon hoë vlakke van sukses en dit is my oortuiging dat hierdie projek die gewenste doelwitte bereik het.

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GENERAL INTRODUCTION

Alien species are plants, animals, pathogens or any other organisms that have established themselves outside their native ranges, be it through deliberate or accidental introduction, and which spread from sites of introduction (Jose et al. 2013; Inderjit 2006; Rotherham and Lambert 2012). The rise of global trade and long-distance transportation have resulted in an exponential increase in the number of invasive species that are recorded globally (Reichard and White 2001; Mack 2005) and, to date, a total of 120 000 species are recorded in just six countries, including South Africa (Pimentel et al. 2005). Although the reasons for species introductions vary, the invasion process is fairly uniform (Richardson et al. 2000). Following introduction, species may become established or naturalised within a particular environment, after which some of them reproduce and spread. This leads them to be classified as invasive species (Richardson et al. 2000; Pyšek et al. 2004). Although the invasion process is fairly well understood, reasons for introduction, the extent of invasion, invasive potential and options for management are species specific (Van Wilgen et al. 2012) and vary accordingly. This requires a broader analysis. Invasive alien plants are widely considered a major threat to biodiversity, and many species also have a massive effect on both human livelihoods and economic development (Kaufman and Kaufman 2013). Plants that become invasive are usually vigorous growers that can outcompete indigenous plants for water, light, space and nutrients (Bromilow 2010).

Tree invasions in South Africa

Trees were only acknowledged as major invasive species during the early 1980's, but there has since been a rapid increase in the number of invasive alien trees, the extent of invasions, and the magnitude and types of impacts in the last few decades (Richardson and Rejmánek 2011). There has, however, been a rapid increase in the number of invasive alien trees, the extent of invasions, and the magnitude and types of impacts in the last few decades (Richardson and Rejmánek 2011; Richardson et al. 2014). A recent global review of invasive alien trees and shrubs listed 751 species from 90 families (Rejmánek and Richardson 2013). South Africa has a major problem with invasive alien plant species (Richardson et al. 1997; Henderson 2007). By 2010, South Africa had at least 8750 introduced plant taxa, of which 660 were recorded as naturalised and 198 as invasive (Wilson et al. 2013). Many are well established while many others are still in the early stages of invasion (Nel et al. 2004; Mgidi et al. 2007). Woody plant species are very well represented in national and regional lists of invasive plant species in South Africa, and species in the genera *Acacia*, *Hakea*, *Eucalyptus*, *Pinus* and *Prosopis* are the dominant invasive plant species in many parts of the country (Richardson et al. 1997). Most of these species have a long residence time (>100 years), have been widely planted in the country (Wilson et al. 2007; Poynton 2009) In addition, they occur predominantly in natural and semi-natural ecosystems (Richardson et al. 1987; Richardson et al. 1990; Harding and Bate 1991; Holmes and Cowling 1997; Holmes et al. 2008). Many other species of alien trees are much more recent introductions and have either not yet become naturalised or have only recently entered the phase of rapid population growth and spread (Nel et al. 2004; Donaldson et al. 2014). A number of these are also abundant in urban ecosystems rather than natural ecosystems, which results in them requiring an entirely different outlook and management approach (Gaertner et al. 2016). A large invasion debt thus exists (Rouget et al. 2015).

Invasive species in cities

The import and export of goods into and out of cities has resulted in the proliferation of invasive alien species in urban areas (Kowarik 2011) with transport linkages facilitating the introduction and spread of non-native species through diverse dispersal pathways (Dehnen-Schmutz et al. 2007). Non-native organisms are exposed to habitats, soils, and climatic and hydrological conditions that have been altered through human activities (Gaertner et al. 2016). If species are pre-adapted to conditions similar to those that exist in their native range, rapid proliferation of newly-established species often takes place (Pickett et al. 2001; Kowarik 2011). Ornamental invasive tree species found in gardens often propagate rapidly, spreading throughout urban ecosystems and displacing the indigenous flora (*Acacia elata*, for example) (Alston and Richardson 2006; Foxcroft et al. 2008). Damage to human infrastructure is also common (*Ailanthus altissima*, for example) (Kowarik and Säumel 2007). These are just some of the many problems associated with invasive species in urban ecosystems (see van Wilgen and Scott 2001 and Gaertner et al. 2016 for other examples). In addition, there are problems with urban invaders in that they often spread into adjoining natural and semi-natural areas (Alston and Richardson 2006; Bowers et al. 2006), displacing and outcompeting native species. The wildland/urban interface in many areas is threatened by a variety of 'edge effects' and is especially vulnerable to invasion by introduced plants that spread from suburban gardens (Alston and Richardson 2006).

Managing invasive species

The South African Department of Environmental Affairs is responsible for the administration of the National Environmental Management: Biodiversity Act (NEMBA), 2004 (Act No. 10 of 2004) and the Alien and Invasive Species Regulations published in 2014 in terms of section 97(1) of the Act prescribe how invasive species should be managed and controlled. According to the Regulations, invasive species are placed into one of four categories (Wilson et al. 2013) with each requiring a different management approach. The following four categories are identified: category 1a invaders require compulsory control through eradication and removal (*Acacia paradoxa*, for example); category 1b invaders require compulsory control as part of an invasive species control programme (*Ailanthus altissima*, for example); category 2 invaders are regulated by area with a demarcation permit required to import, possess, grow, breed, move, sell or buy them (*Nasturtium officinale*, for example); category 3 invaders are species that can remain in your garden. However, you cannot propagate or sell these species and must control them in your garden (*Acer buergeranium*, for example). This legislation places obligations upon all landowners with respect to the effective management of invasive species (Gaertner et al. 2016). Management of invasive species is, however, not an easy undertaking. Limited resources mean that control efforts need to be carefully prioritised (Nel et al. 2004). Determining the current extent of invasions as well potential future distributions enables the prioritisation of management and control efforts (van Wilgen et al. 2011; 2012) ultimately ensuring higher levels of success.

There are three broad approaches to managing invasive species: 1) prevention of introduction; 2) eradication of small isolated invasions; and 3) management of established populations through containment, impact reduction or value addition (Wilson et al. 2013). The cheapest and most effective way of limiting the impact associated with invasive species is to prevent their entry into a country (Leung et al. 2002; Wilson et al. 2013). Prevention may seem relatively straight forward in principle, but very few prevention plans have been entirely effective. As such, limited resources have been allocated to promote prevention plans (Wilson et al. 2013). It is thus important to detect invasion early and to implement control measures rapidly to prevent widespread impact that will result from the spread of an invasive species (Wilson et al. 2013). In this instance, the implementation of an Early Detection, Rapid Response (EDRR) programme has been especially effective (Pyšek and Richardson 2010).

Early Detection, Rapid Response (EDRR)

Early Detection, Rapid Response (EDRR) efforts increase the likelihood that invasion will be controlled successfully and cost-effectively, ultimately mitigating large-scale negative impacts that may result in the future (Westbrooks 2004). Eradication is one of the priority aims for EDRR programmes (Myers et al. 2000). These rely heavily on public involvement to report sightings of invasive species. Eradication is, however, a very expensive option that has experienced high levels of failure in the past. Accurately determining the full extent (distribution) of an invader is often challenging because of inaccessibility to private land as well as the large area that would need to be inventoried (Gaertner et al. 2016). As such, the population size and extent of a species is often underestimated. An improved solution involves the identification of important areas where search efforts should be focussed, based on habitat suitability predictions (Hulme 2009). This would limit the costs associated with monitoring and management. Highlighting suitable areas for invasion will improve search efficiency, reduce costs and enable early detection of populations before they spread (Kaplan et al. 2014). The use of Species Distribution Models (SDMs) and Geographic Information System (GIS) techniques have been helpful in this regard and management efforts have become increasingly reliant on the use of both techniques to identify distribution patterns and potential invasion 'hotspots' (Joshi et al. 2004; Hui and Richardson 2017).This was observed in studies of *Melaleuca parvistaminea* (Jacobs et al. 2014) and *Acacia stricta* (Kaplan et al. 2014) in South Africa, and on *Ailanthus altissima* and *Robinia pseudoacacia* in Spain (Cabra-Rivas et al. 2016).

Evaluating invasion potential: the use of species distribution models (SDMs) and Geographic Information System (GIS) techniques

Species Distribution Models (SDMs) have been widely applied to determine the potential range of invasive species (Hui and Richardson 2017). SDMs are numerical tools that combine species occurrence observations with environmental estimates to predict distribution across a variety of landscapes (Elith and Leathwick 2009). Management programmes have become increasingly reliant on SDMs to establish the suitability of given areas for invasive species and their potential to spread within these areas (Thuiller et al. 2005; Elith and Leathwick 2009; Richardson et al. 2010; Cabra-Rivas et al. 2016). Multi-scale modelling that incorporates a variety of distribution drivers over both the native and adventive ranges is known to improve the overall accuracy of potential species distributions (Sutherst and Bourne 2009; Jiménez-Valverde et al. 2011; Václavík and Meentemeyer 2012).

GIS is also helpful in evaluating distribution patterns and correlates that relate to an invasive species' ecological and biogeographical preferences (Pino et al. 2005). Using the knowledge of an invasive species' preferences along with the identification of areas that are probable invasion 'hotspots' helps delimit areas of unlikely invasion potential, ultimately saving money and time (Joshi et al. 2004).

Both SDMs and GIS techniques – although different in approach and utilisation – are central to evaluating the full extent of an invasive species over a variety of landscapes. Using these in combination over multiple spatial scales has exhibited levels of success in previous studies (see Joshi et al. 2004 and Cabra-Rivas et al. 2016) and should, therefore, be utilised and tested in other studies that may yet to be done. However, every invasive species is unique (Rejmánek and Richardson 1996). Accurately establishing the full extent of an invasive species requires an understanding of the factors that have made the species a successful invader globally. This information should be incorporated these into studies in other parts of the world (Colautti and MacIsaac 2004). For example, factors that facilitate the spread of an invasive species in natural ecosystems will be different to the factors that have an influence on urban invasive species (Lake and Leishman 2004; Gaertner et al. 2016). Emerging invaders will also require a different approach compared to established invaders because they have a greater capacity to spread (Mgidi et al. 2007). All these factors should be understood and incorporated if an accurate assessment of the full extent of an invasive species is to be achieved. To date, there have been few studies that have focussed on the multi-scale analysis of an emerging invader in urban ecosystems. This study focusses on one such species.

Study species

Ailanthus altissima Mill. Swingle (Simaroubaceae; tree of heaven) is a deciduous, dioecious tree species that is native to China. It has been widely planted globally and its adventive range now covers all continents except Antarctica (Kowarik and Säumel 2007). The species is a notorious invader in the northern hemisphere (Kowarik and Säumel 2007; Cabra-Rivas et al. 2016), but has yet to replicate such levels of invasion success in some other parts of the world, including South Africa. Trees reach a maximum height of 30 m in temperate zones and 20 m in meridional zones (Hunter 2000; Kowarik and Säumel 2007). The species has a number of characteristics that are typical of successful invasive plant species, including prolific seed production (ca. 350 000 per female tree/year), rapid achievement of (Burch and Zedaker 2003), the ability to withstand harsh environmental conditions, including high levels of atmospheric pollution (Lawrence et al. 1991) and the ability to reproduce vegetatively after disturbance (Bory et al. 1991; Kowarik 1995; Kowarik and Säumel 2007; Constán-Nava et al. 2010). It is a popular ornamental plant in urban centres around the world and has also been widely used for roadside restoration (Kowarik and Säumel 2007; Constán-Nava et al. 2010). In its adventive range *A. altissima* is most common and abundant in urban areas where it mainly occurs in disturbed sites, degraded fields, along roads and in riparian habitats (Kowarik and Säumel 2007; Constán-Nava et al. 2010). The first record of the species in South Africa is from 1834 (Bradlow 1965). Despite its long residence in the country, the species was not widely disseminated until fairly recently.

Current knowledge and possible knowledge gaps

Many studies of *A. altissima* have been published globally. The negative effects associated with the spread of this species are well documented (see for example Bauman et al. 2013, Feret 1985, Gomez-Aparicio and Canham 2008, Singh et al. 2003 and Small et al. 2010). Contrary to the publications that focus on the negative effects, several studies regarding the beneficial nature of *A. altissima* have also been published (see for example Groninger et al. 2007, Huebner et al. 2007 and Mitsch et al. 2001). Extensive research into the negative and positive effects associated with the species leaves very little space to do new research. This study will therefore not cover this issue extensively.

Equally well documented has been the management strategies that have been implemented in the removal of the invasive *A. altissima*. Burch and Zedaker (2003), Kelly (2001) and DiTomaso and Kyser (2007) are just some of the many publications that have reviewed the management options globally. Although covered extensively globally, comparative South African studies are non-existent which creates an opportunity to evaluate the potential management options for *A. altissima* in parts of South Africa.

Although many databases depict the global distribution of *A. altissima*, an accurate review of global distribution of the species, indicating where the species is native, established and invasive (and its potential distribution), is lacking. Added to this is the fact that tracking the historical spread of the species has never been attempted. Thus, much work is needed to fully understand the extent of *A. altissima* invasions globally.

It is interesting to note that no studies focussing entirely on *A. altissima* have been completed in South Africa. National databases depicting the species' distribution in South Africa are irregularly updated which results in an inaccurate depiction of the species' invasive distribution in our country. Added to this, potential future distribution has not yet been considered which means that the full invasive potential of this species in South Africa has not been considered. Numerous studies on *Acacia saligna*, *A. mearnsii* and *Melia azedarach*, for example, have been completed which creates an opportunity to study a newly-emerging urban invader such as *A. altissima*.

Research objectives

This project had numerous aims and objectives, the ultimate goals being to establish the full extent of *A. altissima* invasion in South Africa and to evaluate potential options for management. A multi-scale analysis (global, country and regional scales) was carried out to examine the current distribution of the species and to determine its potential distribution. This approach was important as it enabled us to gain an insight into the biology of *A. altissima* with specific focus on the factors that influence its spread.

Chapter 1 assesses the biogeography, distribution and habitat suitability of *A. altissima* by evaluating the current and potential distribution (based on climatic suitability) at both a global scale and a national scale (South Africa). The potential distribution that was determined at both spatial scales serves as a first approximation of potential species spread, based solely on the effects of climate.

Chapter 2 evaluates the degree of range filling exhibited by the *A. altissima* in South Africa. It also identifies areas that are at risk of future invasion. Chapter 2 evaluates: 1) the degree of range filling exhibited by the species in South Africa; 2) identifies noticeable differences between the model outputs at a global and country scale; 3) determines the most influential drivers affecting the distribution of *A. altissima* at both spatial scales; and 4) identifies areas that are at risk of future invasion by *A. altissima* in South Africa. The methodology implemented in Chapter 2 drew substantially on the study by Cabra-Rivas et al., (2016), but a larger number of environmental variables and different statistical algorithms were used to compute the models used in this study.

Chapter 3 evaluates the distribution pattern of *Ailanthus altissima* – an Early Detection, Rapid Response (EDRR) target species in South Africa – within the City of Cape Town. The ultimate aim of this chapter is to develop a management protocol for the species by evaluating its distribution at a fine scale. Chapter 3: 1) evaluates the current distribution of *A. altissima* in the City of Cape Town; 2) identifies whether there are clear ecological and biogeographical trends that influenced the distribution of the species, and 3) the using one suburb as a case study, determines potential options for managing *A. altissima* at a city scale.

Chapter 4 provides a summary of overall conclusions of the work undertaken in the dissertation.

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CHAPTER 1: THE PROGNOSIS FOR AILANTHUS ALTISSIMA (SIMAROUBACEAE; TREE OF HEAVEN) AS AN INVASIVE SPECIES IN SOUTH AFRICA; INSIGHTS FROM ITS PERFORMANCE ELSEWHERE IN THE WORLD.

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1.1 Abstract

The rise of global trade and long-distance transportation has resulted in an increase in the number of invasive species globally. South Africa has a major problem with invasive plant species. Many have long residence times, are well established and have large invasive ranges, whereas others are still in the early stages of invasion. Data on the current extent of invasions and potential future invasions by recent arrivals are essential inputs to effective management strategies. *Ailanthus altissima* is a major invasive species in many parts of the world and although it has had a long residence time in South Africa, it is yet to replicate the level of weediness and major impacts that have been reported in other parts of its adventive range. We mapped the countries in which *A. altissima* has been reported and evaluated the invasion status of the species in each of these countries. We then mapped the current distribution in more detail for South Africa. The species is known to be present in at least 51 countries and is invasive or problematic in 23 of these countries. *Ailanthus altissima* is present in all South African provinces except Limpopo and is most common and abundant in the Western Cape, Gauteng, Eastern Cape and Free State. Species distribution modelling was applied, using global distribution data, to determine parts of the world, and in particular within South Africa, that are climatically suitable for the species. Climate is the most influential driver affecting the distribution of invasive species globally, and it serves as a good first approximation of potential species spread. Large parts of Africa are likely to be invaded by this species in the future. Seven regions in South Africa were identified as high risk areas for invasion by *A. altissima*. The species is already far too widespread in South Africa for eradication at the national scale to be feasible. A national strategy for managing the species should involve: 1) early detection, rapid response initiatives in areas identified as climatically suitable; and 2) local and regional-scale initiatives based on objective prioritization in terms of feasibility of management success and asset protection.

Keywords Early Detection, Rapid Response; Early stages of invasion; Invasive species; Potential distribution; Species distribution modelling; Tree invasions

1.2 Introduction

Invasive alien species are organisms that were introduced to new regions by human actions and have spread from sites of introduction (Richardson et al. 2000). The rise of global trade and long-distance transportation has resulted in an exponential increase in the number of invasive alien species that are recorded globally (Lockwood et al. 2013). Some invasive species cause ecological and/or economic damage in invaded ecosystems and threaten biodiversity, human-wellbeing and ecosystem functioning (Pyšek and Richardson 2010). Invasive species are a significant component of human-mediated global environmental change and are responsible for many detrimental effects on biodiversity and the economy (Westphal et al. 2008).

Trees were not widely considered as major invasive species until recently, but there has been a rapid increase in the number of invasive alien trees, the extent of invasions, and the magnitude and types of impacts in the last few decades (Richardson and Rejmánek 2011; Richardson et al. 2014). A recent global review of invasive alien trees and shrubs listed 751 species from 90 families (Rejmánek and Richardson 2013).

South Africa has a major problem with invasive alien plant species (Richardson et al. 1997; Henderson 2007). By 2010, South Africa had at least 8750 introduced plant taxa, of which 660 were recorded as naturalised and 559 as invasive (Wilson et al. 2013). Many are well established while many others are still in the early stages of invasion (Nel et al. 2004; Mgidi et al. 2007). Woody plant species are very well represented in national and regional lists of invasive plant species in South Africa, and species in the genera *Acacia*, *Hakea*, *Eucalyptus*, *Pinus* and *Prosopis* are the dominant invasive plant species in many parts of the country (Richardson et al. 1997). Most of these species have a long residence time (>100 years) and have been widely planted in the country (Wilson et al. 2007; Poynton 2009). Many other species of alien trees are much more recent introductions and have either not yet become naturalized or have only recently entered the phase of rapid population growth and spread (Nel et al. 2004; Donaldson et al. 2014); a large invasion debt thus exists (Rouget et al. 2015). Limited resources mean that control efforts need to be carefully prioritized (Nel et al. 2004). Determining the current extent of invasions as well as potential future distributions is vital for the implementation of integrated management plans (van Wilgen et al. 2011; 2012).

There are three broad approaches to managing invasive species: 1) prevention of introductions; 2) eradication of small isolated invasions; and 3) management of established populations through containment, impact reduction or value addition (Wilson et al. 2013). Although preventing the entry of invasive species is the cheapest and most effective way of limiting the impacts associated with invasive species, limited resources are allocated to prevention in most parts of the world (Leung et al. 2002; Wilson et al. 2013). It is thus important to detect invasions early and implement control measures rapidly to prevent widespread impacts that will result from the spread of an invasive species (Wilson et al. 2013). In this instance, the implementation of an Early Detection, Rapid Response (EDRR) programme has been particularly effective (Pyšek and Richardson 2010). EDRR efforts increase the likelihood that invasions will be controlled successfully and cost effectively, ultimately mitigating large scale negative impacts that may result in the future (Westbrooks 2004). Eradication is one of the priority aims for EDRR programmes (Myers et al. 2000), however, this option is often expensive and has a high probability of failure. An improved solution involves the identification of important areas where search efforts should be focussed, based on habitat availability and climatic suitability predictions (Hulme 2009), to limit the costs associated with monitoring and management. Highlighting suitable areas for invasion will improve search efficiency, reduce costs and enable early detection of populations before they spread (Kaplan et al. 2014). This was observed in studies that were done on *Melaleuca parvistaminea* (Jacobs et al. 2014) and *Acacia stricta* (Kaplan et al. 2014) in South Africa. South Africa has progressive legislation for regulating invasive alien species, notably the National Environmental Management Biodiversity Act (NEM:BA Act 10 of 2004). NEM:BA provides the impetus and legal underpinning for the management of invasive plants in South Africa, focusing on the three broad approaches mentioned above.

There is much to learn about the invasive potential of a given species within a particular area by looking at the invasion ecology of the species in other areas (e.g. Richardson et al. 2008; 2015). Besides dealing with current widespread invasive species, it is also important to identify those invasive species that have become major weeds globally (especially in regions with similar climatic and environmental conditions to those that exist in the area in question) but which have not yet replicated such levels of invasion. This paper focusses on assessing the biogeography, distribution and habitat suitability of *Ailanthus altissima*; a tree native to China which has been introduced to many parts of the world (Kowarik and Säumel 2007). The species is currently a widespread invasive species throughout Europe (Kowarik and Säumel 2007; Cabra-Rivas et al. 2015) and the United States, particularly in urban areas (Albright et al. 2010). Its distribution and introduction status in other regions to which it has been introduced have been much less thoroughly assessed. The aim of this paper is to review the distribution/status of *A. altissima* following its introduction to areas outside its native range globally and to assess its current and potential status in South Africa. Current invasion hotpots of *A. altissima* in South Africa are identified and predictions are made regarding its potential range in the country. Such insights are needed to inform national, regional and local-scale strategies to manage the species.

1.3 Methods

1.3.1 Study species

Ailanthus altissima Mill. Swingle (Simaroubaceae; tree of heaven) is a deciduous, dioecious tree species that is native to China but has been introduced to all continents except Antarctica (Kowarik and Säumel 2007). Trees reach a maximum height of 30 m in temperate zones and 20 m in meridional zones (Hunter 2000; Kowarik and Säumel 2007). The species has many characteristics typical of successful invasive species (Berger 1993; Bright 1995; Knapp and Canham 2000). Female trees produce large numbers of seeds (ca. 350 000 per female/year) that are dispersed during spring (Burch and Zedaker 2003). Sprouts as well as seedlings show rapid achievement of maturity within the first year of their development (Burch and Zedaker 2003) often forming dense stands. *Ailanthus altissima* is extremely hardy and tolerates harsh weather conditions and high levels of atmospheric pollution (Lawrence et al. 1991). It establishes easily, grows fast and reproduces prolifically from seeds and vegetatively after disturbance (Bory et al. 1991; Kowarik 1995; Kowarik and Säumel 2007; Constán-Nava et al. 2010). It is a popular ornamental plant in urban centres in many parts of the world and has also been widely used for roadside restoration (Kowarik and Säumel 2007; Constán-Nava et al. 2010). In its adventive range *A. altissima* is most common and abundant in urban areas where it mainly occurs in disturbed sites, degraded fields and along roads and water courses (Kowarik and Säumel 2007; Constán-Nava et al. 2010). In South Africa, *A. altissima* occurs predominantly in urban and suburban areas with regulations preventing any further planting of the species (Henderson 2007). Although it has a long residence time in South Africa (Henderson 2006), *A. altissima* has yet to replicate similar levels of invasion success that are observed in countries throughout its adventive range.

1.3.2 Assessment of the global distribution of *Ailanthus altissima*

A global map was created in ArcMap 10.3.1 to show the countries in which *A. altissima* is native, alien, naturalized and invasive. Distribution data were collated from many sources; the Global Biodiversity Information Facility (GBIF), Centre for Agriculture and Biosciences International (CABI), the Global Invasive Species Database (GISD) and Delivering Alien Invasive Species Inventories for Europe (DAISIE) were the primary sources of data. Data were also sourced from a search of the literature and the internet. After editing to remove obviously incorrect localities (e.g. from the ocean) the final data set comprised 11462 localities.

The term 'invasive' is often used loosely in the literature dealing with alien plant species (Pyšek et al. 2004); this is certainly the case for the data sources and publications dealing with *A. altissima*. It was therefore difficult to discern the precise introduction status of *A. altissima* at all localities in its adventive range [i.e. the position of introduced populations on the introduction-naturalization-invasion continuum as conceptualized by Richardson and Pyšek (2012)]. We categorized all data points following the criteria proposed by Pyšek et al. (2004) and Richardson et al. (2011) as follows: "native" (within the native range); "alien only" (all records outside the native range where there is no evidence of naturalization or invasion); "naturalized" (where there is evidence of localised reproductions with a number of presence points occurring within a confined area); "widely invasive" (countries where the species has spread substantial distances from initial introduction sites and where at least five publications/online sources identify *A. altissima* as an invasive species and/or where we found evidence of at least two active management programmes targeting *A. altissima*). To identify countries that fall under one of the above-mentioned categories, we used a variety of search engines including Google, Google Scholar and Web of Science. We searched for the global distribution of *A. altissima* as well as its invasion status in each of the recorded countries, and cross checked these numerous times to ascertain validity.

1.3.3 Distribution in South Africa

We mapped the current distribution of *A. altissima* in South Africa using all available data sources. A total of 88 high-precision records recorded to the nearest second using a GPS were available from the South African Plant Invaders Atlas (SAPIA) database (for details of SAPIA, see Henderson 1998). Additional data were obtained from the City of Cape Town's Invasive Species Unit, the South African National Biodiversity Institute's (SANBI) Invasive Species Programme (ISP), several herbaria, and from the online biodiversity website iSpot (http://www.ispotnature.org/). Additional data points were collected during random surveys that took place in urban centres in the Western Cape, Gauteng and KwaZulu-Natal provinces during 2015. An article published in the popular magazine *Veld & Flora* (December 2015 issue) yielded 12 new locality records. Records were edited to remove duplicates and obviously erroneous entries. 375 records were thus collated and used to produce a map layer in ArcMap 10.3.1.

1.3.4 Species distribution modelling

All occurrence data that encompasses the native, alien, naturalized and invasive ranges of *A. altissima* were used to develop this model. Many of the records for this species are from urban areas which are highly modified environments (Picket et al. 1997; Grimm et al. 2008). This could lead to prediction errors in the model such as over- or under-estimation of the potential range (Fielding and Bell 1997). For this study, however, we identified the potential range of the species based solely on climate as a first approximation in defining the potential range of the species. All duplicate records in 10-minute grid cells were removed; this left 4644 unique values for the global data set, and 375 for the South African data set. Maximum Entropy Modelling (MaxEnt) was used to identify the potential range of *A. altissima* based on climatic suitability. MaxEnt takes as input a set of layers or environmental variables (such as climate in this instance), as well as a set of georeferenced occurrence locations, and produces a model of the potential range of any given species (Phillips et al. 2006). The software evaluates the suitability of each grid cell as a function of all environmental variables in that cell (Ficetola et al. 2007) and provides a suitability value that ranges from 0 (unsuitable) to 100 (optimal) (Phillips et al. 2006). Recent comparisons have shown MaxEnt to be the most effective method for predicting species distribution using presence-only data (Ficetola et al. 2007). Five climatic variables at 10 arc-minute spatial resolution were downloaded from WorldClim (http://www.worldclim.org/). We used the following climatic variables: maximum temperature of the warmest month; minimum temperature of coldest month; precipitation of wettest month; precipitation of driest month, and precipitation seasonality (coefficient of variation). *Ailanthus altissima's* ability to tolerate a broad range of climatic conditions (Kowarik and Säumel 2007) provided reasoning for the selection of these five climatic variables. Additionally, other studies that focussed on modelling the potential distribution of *A. altissima* in other parts of its adventive range used similar climatic parameters (see Albright et al. 2010; Cabra-Rivas et al. 2016). MaxEnt user-specified parameters and their default values were used to develop this model; these include: convergence threshold = 10^{-5}, maximum iterations = 1000, regularization value β = 10^{-4}, and the use of linear, quadratic, product and binary features (Phillips et al. 2006).

1.4 Results

1.4.1 Current global distribution

Ailanthus altissima is native to China (Fig. 1.1). Several studies have added northern Vietnam to the native range of the species (Kowarik and Säumel 2007), but most publications and online databases delimit the native range within China (see Miller 1990; Knapp and Canham 2000; Ding et al. 2006). The species has been very widely moved around the world and is now alien in at least 51 countries. We used a higher number of online publications and databases to establish the adventive range of *A. altissima* and as such, the adventive range that we have delimited in this study may be slightly larger than the range depicted in the study by Kowarik and Säumel (2007). We found evidence of *A. altissima* naturalization in 48 countries globally, and it is clearly invasive in 23 countries. *Ailanthus altissima* is most prolific and widespread as an invasive species in Europe (25 countries and 54% of the total alien range). This is followed by Asia with 13 countries; including Israel, Turkey, Armenia and Palestine in the Middle-East. *Ailanthus altissima* is listed as an alien species in six African countries (South Africa, Lesotho, Algeria, Tunisia, Morocco and Libya), two South American countries (Chile and Argentina) and in Australia and New Zealand. The species is listed as an alien species in three countries in Central and North America: Canada, Mexico and the United States of America.

Of the 51 countries in which we determined *A. altissima* to be an alien tree species, 23 were identified as invasion hotspots in which the species occurs as a widespread invader (Fig. 1.1). *Ailanthus altissima* is widely invasive throughout most of Europe with 16 of the 23 countries where it is listed as invasive all occurring within the European Union (EU). *Ailanthus altissima* is extensively invasive in four Asian countries (including Israel in the Middle East) and Australia, South Africa and the USA.

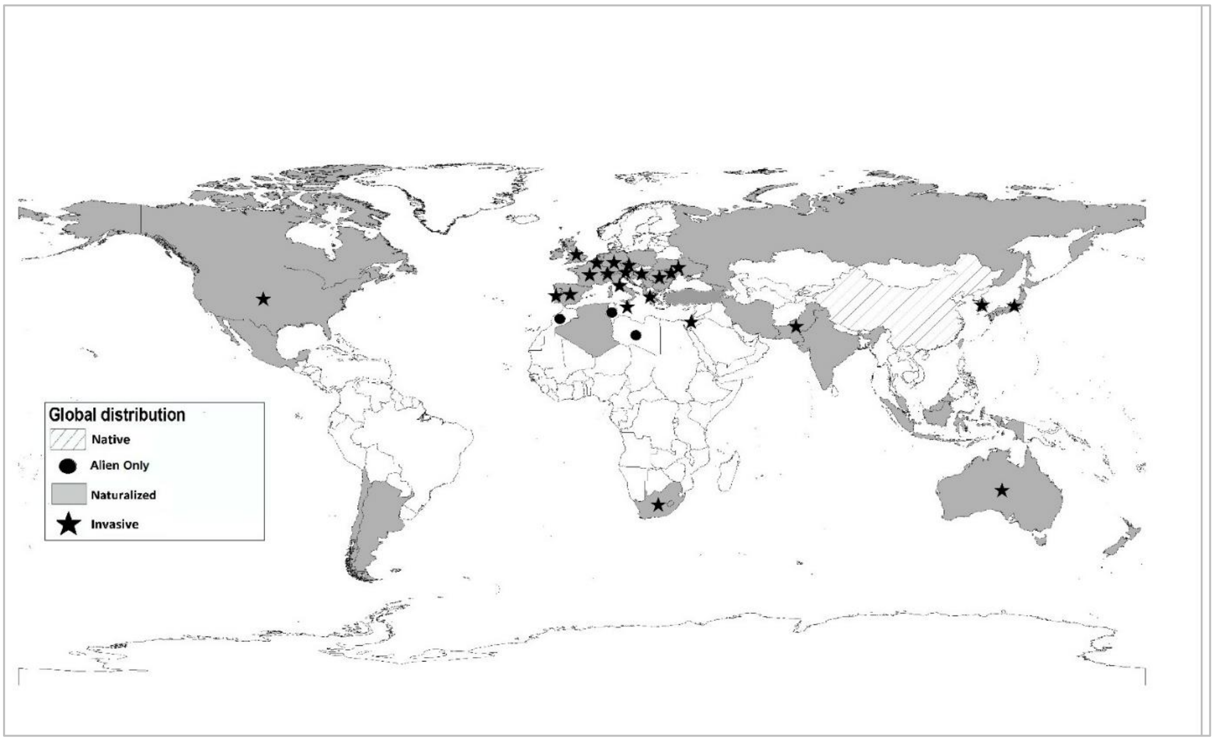

Figure 1.1: The current global distribution of *Ailanthus altissima* showing the native and alien ranges and countries where the species is widely invasive. “Alien only” denotes countries where the species is recorded but where there is no evidence of naturalization or invasion.

1.4.2 Potential global distributionBoth the northern and southern temperate zones appear most suitable for future *A. altissima* invasion (Fig. 1.2). No areas within the equatorial zone are climatically suitable for the species. A large portion of Europe – ending towards the western boundary of Russia - appears to be climatically suitable for the species. With the exception of the southern regions of Norway and Sweden, the rest of Europe that falls within the climatically suitable range already have naturalized populations of *A. altissima*.

Large portions of Mexico and the USA appear to be suitable for *A. altissima* invasion, as do the eastern parts of Canada. These regions currently all have naturalized populations of *A.*

altissima. In South America, Argentina, Bolivia, Chile, Peru, and the southern portion of Brazil all appear to be suitable for future invasion. Currently Argentina and Chile are the only two countries for which we found records of naturalized populations of *A. altissima* in South America, suggesting that the species has much potential for expanding its. Most of southern Africa appears to be climatically suitable for invasion, as do the extreme northern parts of Africa. In particular, Botswana, Namibia, Morocco, Lesotho, Swaziland and Zimbabwe all appear to be susceptible to invasion. Africa appears to be the most susceptible continent for future *A. altissima* invasion; as far as we know the species is only naturalized in three African countries and present in another three. Most of central Asia including Nepal, Mongolia, South and North Korea and Japan, all appear to be climatically suitable for *A. altissima*. Eastern parts of Australia as well as New Zealand appear to be highly climatically suitable, but Western Australia appears to be only moderately climatically suitable.

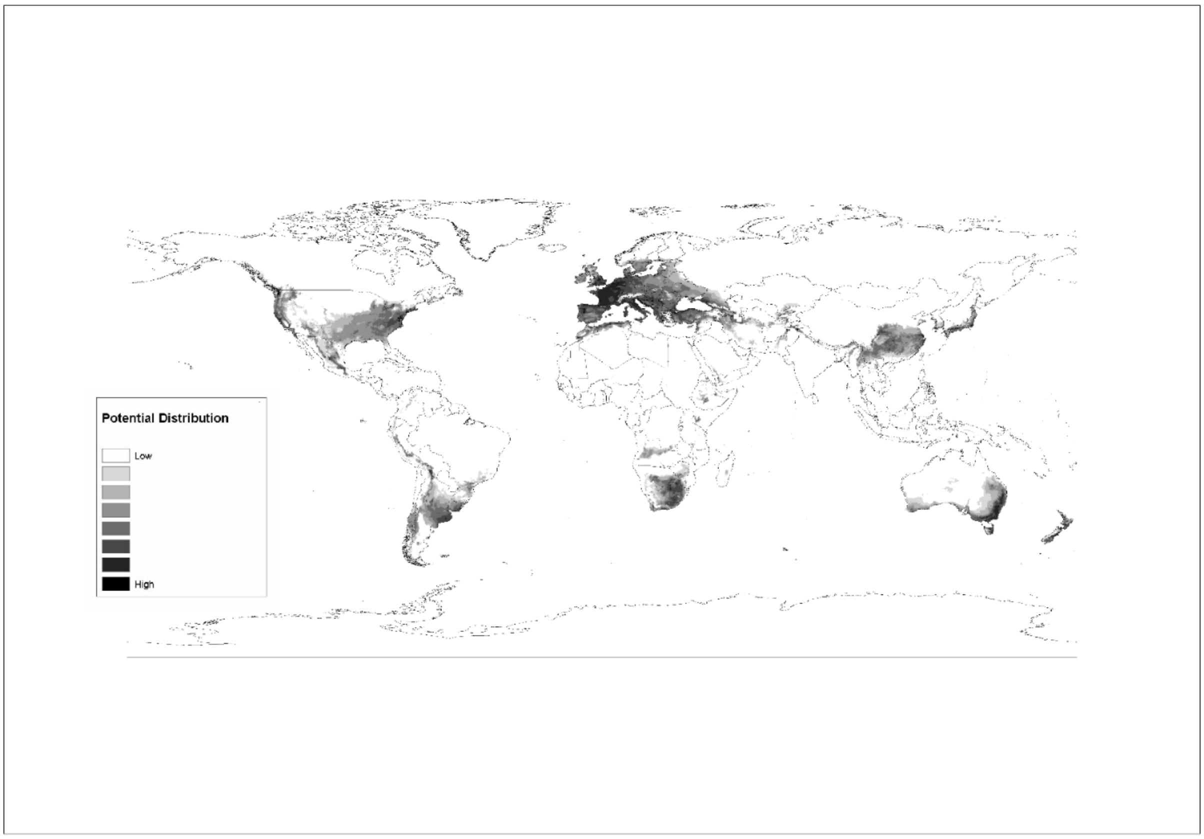

Figure 1.2: The potential distribution of *Ailanthus altissima* based on climatic suitability.

1.4.3 Current and potential distribution in South Africa

Within South Africa, *A. altissima* is most abundant and widespread throughout the province of Gauteng (Fig. 1.3). It is also fairly widespread in the southwestern part of the Western Cape, especially in and around the cities of Cape Town and Knysna; and in the Eastern Cape, Free State (especially along the border with Lesotho) and Mpumalanga provinces. It has a scattered distribution in the North West and Northern Cape provinces. I found two records from KwaZulu-Natal.

A number of areas can be identified as likely localities for future *A. altissima* invasions based on climatic suitability: 1) central Western Cape, 2) central North West, 3) central to eastern region of the Limpopo province, 4) eastern regions of the Mpumalanga province bordering Gauteng, 5) northern regions of KwaZulu-Natal near the borders with the Free State and Mpumalanga, 6) central to northern Eastern Cape; and 7) coastal regions in parts of the Eastern and Western Cape provinces near the town of Knysna.

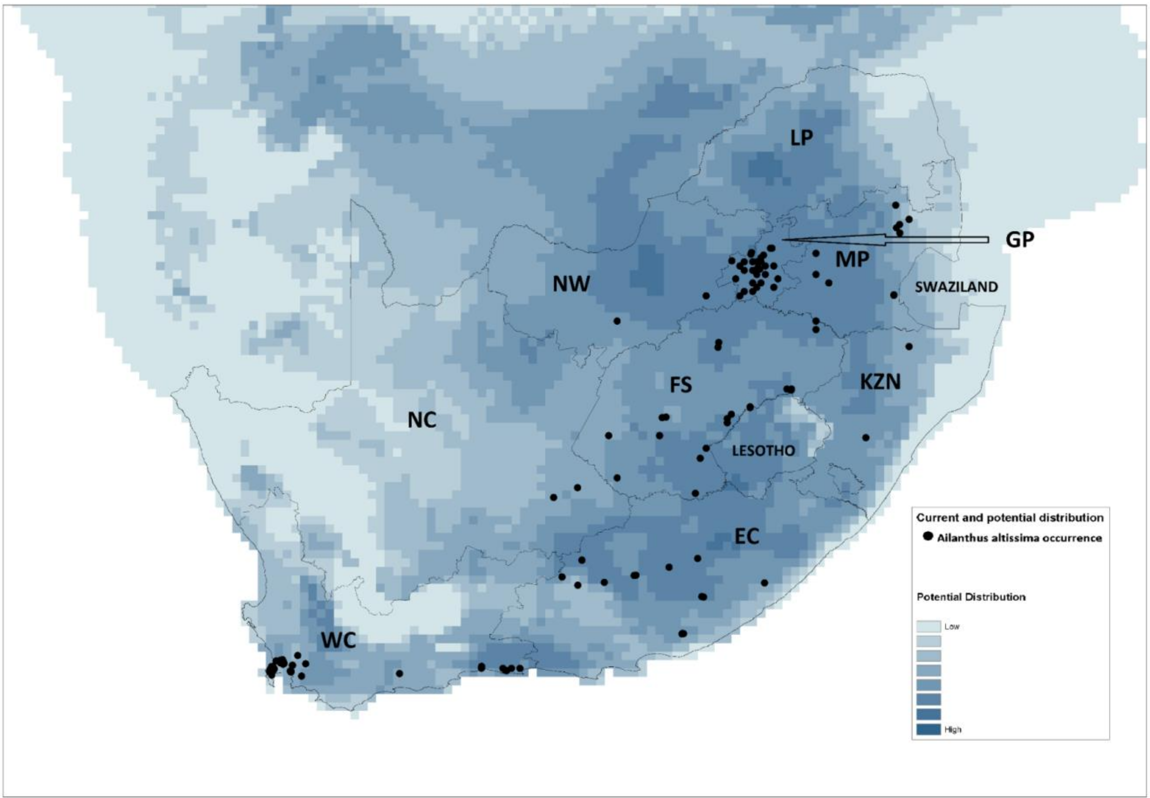

Figure 1.3: The current distribution of *Ailanthus altissima* in South Africa (dots) and the potential range of the species based on climatic suitability derived from species distribution modelling using global locality data. WC = Western Cape; NW = North West Province; LP = Limpopo; MP = Mpumalanga; GP = Gauteng; KZN = KwaZulu-Natal; EC = Eastern Cape.

1.5 Discussion

1.5.1 Current global distribution

The native range of *A. altissima* covers large portions of China where the species occurs as a natural component of broadleaf forests (Kowarik and Säumel 2007). The species' adventive range extends across all continents except Antarctica. *Ailanthus altissima* has spread rapidly throughout the western world (Burch and Zedaker 2003), facilitated by human mediated transfer of seeds and widespread plantings as an ornamental tree and for various restoration purposes. The earliest known introductions took place in Japan and Korea, where records suggest that the species is not native (Little 1979). Most Asian countries surrounding China (13 in total) have records of naturalized *A. altissima* populations. It is likely that cross-border transport of seeds and root and stem fragments resulted in the species spreading and establishing in these countries (Shafiq and Nizami 1986), but records do not give dates of introduction. Israel and Pakistan are the only exception to this as records show that the species was deliberately planted in both countries during the mid-1900s (Rottenberg 2000; Marwat et al. 2010). Both countries are located in the temperate zone and have similar climatic conditions (Kottek et al. 2006).

Ailanthus altissima was introduced to Europe in 1751 (Feret 1985) and has spread across the European Union (Bacon et al. 2012). Until the 1980s, the species colonized parts of central Europe with warmer summers, but it has now colonized cities with colder climates in addition to coastal cities (Sudnik-Wojcikowska 1998; Tokarska-Guzik 2005; Kowarik and Säumel 2007). Within urban areas in Europe, *A. altissima* is mostly confined to inner-city areas, although in warmer parts of Europe the species is common in both cities and rural sites (Kowarik and Säumel 2007).

The spread of *A. altissima* in North America came from three deliberate introductions (Burch and Zedaker 2003). The species is currently invasive in 31 states of the USA and occurs across a broad range of elevations and climatic conditions (Feret 1985). The North American distribution pattern differs significantly to that in Europe, with *A. altissima* colonizing a broad habitat range that includes eastern hardwood forests (Kowarik and Säumel 2007) and cities (Pan and Bassuk 1986). The species has also spread into both

Canada and Mexico where it is naturalized (Meloche and Murphy 2006). Very little work has been done on *A. altissima* elsewhere in its adventive range.

1.5.2 Potential global distribution and invasion debt

Species distribution modelling is central to both the fundamental and applied research sectors of biogeography (Araujo and Guisan 2006). Although the use of species distribution models to determine the potential range of an invader has been well publicised (Gallien et al. 2012; Cabra-Rivas et al. 2016), selecting which environmental variables to use at which spatial scale has always been a contentious issue (Guisan and Thuiller 2005). Climate is a key factor that defines the range limits of invasive species globally (Theoharides and Dukes 2007) and as such, it is important to incorporate climatic variables when determining the potential range of an invasive plant species (Kriticos et al. 2003). Other factors such as biotic interactions with native communities, human influence and the ability to disperse also influence the outcome of introductions at local scales (Ficetola et al. 2007). Climatic variables are, however, widely used to develop distribution models of a species as a first approximation of potential species distribution (Pearson and Dawson 2003; Richardson and Thuiller 2007).

Ailanthus altissima can tolerate a broad range of climatic conditions although seasonal variation in temperature affects the survival, growth and spread of the species (Kowarik and Säumel 2007). Both the native and adventive ranges have climatic conditions characterized by lengthy, warm growing seasons, regular winter frost and annual precipitation of at least 500 mm (Kowarik and Säumel 2007). There was a high degree of consistency between the current distribution of *A. altissima* and the potential climatically derived range of the species.

Ailanthus altissima is currently naturalized in three African countries (South Africa, Lesotho and Algeria). However, based on climatic suitability, Africa appears to be the continent most susceptible to future invasion. Southern Africa, including Botswana, Namibia, Swaziland and Zimbabwe, appears to be the region most susceptible to invasion. Large areas of land within each of these listed countries are arid or semi-arid and will thus be unsuitable to invasion by *A. altissima* in the future. The only country outside southern Africa that appears to be highly susceptible to *A. altissima* invasion is Morocco. Isolated areas in Ethiopia, Kenya, Burundi, Malawi, Tanzania, central Angola and the Democratic Republic of the Congo appear to be moderately susceptible to invasion. All the countries that are most susceptible border at least one of the three countries that currently have naturalized populations of *A. altissima.* This increases the possibility of cross-border introductions of the species (Faulkner et al. 2016). In North Africa, the coastal and central region of Morocco (north of the Atlas Mountains) is the most susceptible area for *A. altissima* invasion. The climatically suitable range encompasses all of Morocco's largest cities: Casablanca, Fès, Marrakesh, Rabat, and Sale. Surveys in urban and natural environments are required to ensure the early detection of *A. altissima* establishment in this region.

1.5.3 Current and potential distribution in South Africa

South Africa has six broad climatic zones: 1) cold interior, 2) temperate interior, 3) hot interior, 4) temperate coastal, 5) sub-tropical coastal and 6) arid interior (Conradie 2012). *Ailanthus altissima* is currently confined to the temperate coastal zone in the Western Cape and is split between the sub-tropical coastal and temperate interior zones in the Eastern Cape. The remainder of the current range falls within the cold interior and temperate interior zones which include large parts of both the central high plateau (Highveld) and the Great Escarpment.

The species occurs along the northern and western borders of Lesotho where it is abundant. It was previously cultivated in Lesotho for rehabilitation of erosion gullies, and as a common rangeland tree (Leslie et al. 1992). Cross border spread of the species into South Africa in the absence of border control policies (Peberdy 2001) resulted in the current distribution pattern. Active cultivation of the tree is no longer undertaken in Lesotho (Leslie et al. 1992). A clustered population occurs in the north-eastern part of Mpumalanga which borders the Kruger National Park (KNP). Most of the invasive alien plant species in the KNP were either introduced unintentionally along rivers and roads, or intentionally for use as ornamental plants (Foxcroft et al. 2008).

The potential distribution of the species seems to correspond with two of the six clusters of invasive alien plants in South Africa defined on geographic distribution (Rouget et al. 2015): cluster 1 (species that are predominantly confined to the grassland biome) and cluster 6 (species that commonly occur in the fynbos biome). *Ailanthus altissima* predominantly invades urban areas in large parts of its invasive range (Heisey 1996; Webster et al. 2006; Kowarik and Säumel 2007). Consequently, it is difficult to evaluate its current broad distribution compared to the patterns of the 'alien biomes' defined by Rouget et al. (2015) on the basis of distribution patterns for invasive plants that mostly invade natural vegetation. Anthropogenic factors did not emerge as being important in separating clusters for the 69 invasive plants included in the study Rouget et al. (2015). *Ailanthus altissima* is well adapted to thrive in human-modified environments and as such, further work is required to elucidate how factors associated with human-dominated landscapes interact with broad climatic factors to define habitat suitability for this species in South Africa.

There is a strong correlation between the current distribution of *A. altissima* in South Africa and the climatically-derived potential range based on the global distribution of the species. *Ailanthus altissima* is, however, absent from some potentially highly suitable sites. The species has had a long residence time in South Africa (Henderson 2006) which suggests that several factors could have limited the spread of the species. These could include the possibility that *A. altissima* has had a limited ability to spread from seed in South Africa or that female trees were historically selected for cultivation over male trees due to the unpleasant odour that males of the species give off (Miller 1990). More work is required to quantify the factors that influence range limits of the species in South Africa. Nonetheless, the large number of locality records used from the northern hemisphere, including both natural or semi-natural habitats and urban locations, probably integrates the broad-scale habitat requirements of the species adequately to allow for a preliminary assessment of the potential of the species to expand its range further in South Africa. We therefore predict substantial further spread of this species which is still categorized as an emerging invader in the country (Wilson et al. 2013). Containment and impact reduction are the most appropriate tactics for emerging invaders, the ultimate goal being to reduce the measurable impacts to acceptable levels in invaded areas and to prevent spread of the species into unoccupied areas (van Wilgen et al. 2011). In terms of spatial prioritization it is important to: 1) focus on eradication in sparsely populated areas, and 2) prioritize control efforts in high-impact areas (van Wilgen et al. 2011).

1.6 Conclusions

The species is widespread and abundant throughout Europe however the current distribution in Europe matched the potential, climatically derived range suggesting that there is very little room for further spread. There is however a large capacity for potential spread Africa and cross-border introductions need to be kept to a minimum to prevent this from happening. In South Africa, the species is predominantly confined to urban areas and based on climatic suitability predictions, there appears to be a large capacity for further spread throughout the country. The use of various online databases to acquire occurrence data for a particular species is beneficial and largely accurate however some of these databases do need to be updated and monitored to prevent the appearance of any erroneous data. Climate has a major influence on shaping the distribution of invasive species at a broad scale and as such, modelling the potential distribution of an invader using climatic variables alone serves as a good first approximation of potential species spread. This approach can however be improved upon by incorporating other influential drivers of invasion (such as land use and human mediated disturbances) to accurately quantify the potential spread of an invasive species.

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CHAPTER 2: ASSESSING THE POTENTIAL RANGE OF *AILANTHUS ALTISSIMA* (SIMAROUBACEAE; TREE OF HEAVEN) IN SOUTH AFRICA: THE ROLE OF CLIMATE, LAND USE AND DISTURBANCE

Target journal for publication: Biological Invasions (invited paper for special issue on invasions in urban ecosystems).

2.1 Abstract

Invasive plant species are problematic in South Africa. A number of species are well established whereas others are still in the early stages of invasion. Control and eradication of invasive alien species is most cost effective at the early stages of invasion. Management programmes have become increasingly reliant on the use of species distribution models (SDMs) that combine species occurrence observations with environmental estimates to predict distributions across a variety of landscapes. The aim of this study was to determine the degree to which *A. altissima* has occupied its potential range in South Africa, so as to identify areas at risk of future invasion. To do this I built a set of ensemble models at both global (10 arc-minute spatial resolution) and national scales (5 arc-minute spatial resolution) using climatic, land use and human-footprint data. Climatic data were most able to explain the distribution of *A. altissima* at the global scale whereas human-mediated disturbances were the most influential explanatory variables at the national scale. My analyses also highlighted the importance of human-mediated disturbances at a global scale and human inhabitancy at a national scale. I conclude that *A. altissima* populations are already present in most areas identified as being environmentally suitable for the species in South Africa, and that management actions should focus on preventing increases in density in these areas.

Keywords

Biological invasions; Ensemble models; Invasive species; Early stages of invasion; Range filling; Species distribution models; Spread potential; Tree invasions

2.2 Introduction

South Africa has a major problem with invasive alien plant species (Richardson et al. 1997; Henderson 2007). Many species are well established and many others are still in the early stages of invasion (Nel et al. 2004; Mgidi et al. 2007; Wilson et al. 2013). Woody plant species are very well represented in national and regional lists of invasive plant species in

South Africa, and species in the genera *Acacia*, *Hakea*, *Eucalyptus*, *Pinus* and *Prosopis* are the dominant invasive plant species in many parts of the country (Richardson et al. 1997). Many other species of alien trees are either recent introductions or have not enjoyed widespread dissemination. Some of these species are known invaders in other parts of the world, or have attributes associated with invasiveness, but have not yet expressed their invasive tendencies in South Africa. Some have not yet become naturalized, while others only recently entered the phase of rapid population growth and spread (Nel et al. 2004; Donaldson et al. 2014); a large invasion debt thus exists (Rouget et al. 2015).

Control of invasive alien species (IAS) is most effective at the early stages of invasion (Wittenberg and Cock 2005; Wilson et al. 2016). Early detection and management mitigates widespread impacts associated with the future spread of certain IAS (Wilson et al. 2013, 2016). Species distribution models (SDMs) have been widely applied to determine the potential range of invasive species (Hui and Richardson 2017). SDMs are numerical tools that combine species occurrence observations with environmental estimates to predict distributions across a variety of landscapes (Elith and Leathwick 2009). Management programmes have become increasingly reliant on SDMs to establish the suitability of given areas for particular invasive species and their potential to spread within these areas (Thuiller et al. 2005; Elith and Leathwick 2009; Richardson et al. 2010; Cabra-Rivas et al. 2016).

The suitability of SDMs for modelling the potential ranges of invasive species is however debatable (Guisan and Thuiller 2005; Gallien et al. 2010, 2012; Gassó et al. 2012; Cabra-Rivas et al. 2016). This is because SDMs that are used to model the potential ranges of IAS assume that the environmental conditions in the species' native range are the same as those in its adventive range (Gallien et al. 2012) and that the species being modelled is at quasi-equilibrium with the environment in which it occurs (i.e. the species is established at all suitable sites and is absent from all unsuitable sites) (Guisan and Thuiller 2005). For this reason, it has been suggested that all available global data from both the native and invasive ranges of the invasive species should be used in determining the "ecological niche" of introduced species (Beaumont et al. 2009; Ibáñez et al. 2009; Gallien et al. 2012). The ecological niche refers to relationships between an invasive organism and its physical and biological environment, which accounts for the effects of both time and space (Shea and Chesson 2002). Such an approach does not, however, account for particular conditions that characterize local ranges (e.g. environment, interactions and human uses) (Gallien et al. 2012). Multi-scale modelling that incorporates a variety of distribution drivers over both the native and adventive ranges is known to improve the overall accuracy of potential species distributions (Sutherst and Bourne 2009; Jiménez-Valverde et al. 2011; Václavík and Meentemeyer 2012). With this in mind, Cabra-Rivas et al. (2016) integrated various SDMs from multiple scales to establish the relative importance of various drivers in shaping the distribution of two invasive tree species. They found that climatic variables were the main contributors to the global and country-scale models for both species, followed by land use. The prevalence of climate over land use as an explanatory variable for distribution could be because of the climatic heterogeneity within the studied region - the opposite situation could exist in a climatically homogenous region (Cabra-Rivas et al. 2016). At a finer scale, however, human-mediated disturbances were more influential than either climate or land use, a finding supported by a number of other authors (e.g., Rouget and Richardson 2003; von Holle and Motzkin 2007; Lambdon et al. 2008).

This paper focuses on the tree of heaven (*Ailanthus altissima*), a widespread invasive species in the northern hemisphere that, for unknown reasons, has yet to become a widespread invader in South Africa. This species is unusual among widespread invasive tree species (see Richardson and Rejmánek 2011 for a global review) in that it is largely an invader of urban habitats (Kowarik and Säumel 2007). This means that climate data of the type typically used to model the range limits of species in SDMs is probably of limited value, since environmental conditions in urban habitats are influenced by diverse human activities. The use of human-influenced environmental factors (such as the human footprint indicator) would have a higher influence on predicting the potential distribution of an urban invader than typical environmental factors (such as climate) and as such, it is imperative to incorporate these into the design of SDM's (Guisan and Thuiller 2005. I aim to evaluate the degree of range filling exhibited by this species in South Africa and to identify areas at risk of future invasion. In a previous study, the current and potential distribution of *A. altissima* was evaluated at a global and country-level spatial scale (for South Africa) (Walker et al., under review). To do this, a simple bioclimatic envelope model was generated in MAXENT. Such bioclimatic models usually provide useful approximation of the potential range of species (Pearson and Dawson 2003; Guisan and Thuiller 2005), but many other factors also influence the distribution of invasive species (Guisan and Thuiller 2005; Cabra-Rivas et al. 2016). Understanding the role of such additional factors is important to inform management strategies. This is particularly important when modelling the spread of invasive species that are not only influenced by natural factors (such as climatic variables) that determine their range limits very broadly, but are also affected by anthropogenic or non-natural factors (such as human-mediated disturbances). Accurately establishing the potential range of species like *A. altissima* requires integration of all the above-mentioned factors (Cabra-Rivas et al. 2016). It is interesting to examine the relative role of climatic and other factors in shaping the potential distribution of *A. altissima* in South Africa where the species – although having a long residence time in country – is yet to replicate similar levels of invasion success as it has in other parts of its adventive range. I address the following questions: (1) To what degree has *A. altissima* expanded its potential range in South Africa?; (2) Are there noticeable differences between the model outputs achieved through modelling the potential distribution of *A. altissima* at a global scale using coarse grain variables (10 arc-minute resolution), and modelling at a national scale using finer-grain variables (5 arc-minute resolution)?; (3) What are the most influential factors that determine the potential spread of *A. altissima* at a global and national scale?; (4) Which areas are at risk of future invasion by *A. altissima* in South Africa?

2.3 Methodology

2.3.1 Study species

Ailanthus altissima Mill. Swingle (Simaroubaceae; tree of heaven) is a deciduous, dioecious tree species that is native to China. It has been widely planted globally and its adventive range now covers all continents except Antarctica (Kowarik and Säumel 2007). The species is a notorious invader in the northern hemisphere (Kowarik and Säumel 2007; Cabra-Rivas et al. 2016), but has yet to replicate such levels of invasion success in some other parts of the world, including South Africa. The species has several characteristics that are typical of successful invasive plant species, including prolific seed production (ca. 350 000 per female tree/year), rapid juvenile growth (Burch and Zedaker 2003), the ability to withstand harsh environmental conditions, including high levels of atmospheric pollution (Lawrence et al. 1991) and the ability to reproduce vegetatively after disturbance (Bory et al. 1991; Kowarik 1995; Kowarik and Säumel 2007; Constán-Nava et al. 2010). It is a popular ornamental plant in urban centres around the world and has also been widely used for roadside restoration (Kowarik and Säumel 2007; Constán-Nava et al. 2010). In its adventive range *A. altissima* is most common and abundant in urban areas where it mainly occurs in disturbed sites, degraded fields, along roads and in riparian habitats (Kowarik and Säumel 2007; Constán-Nava et al. 2010). The first record of the species in South Africa is from 1834 (Bradlow 1965). Despite the fact that it has been in South Africa for a long time, it has not been widely disseminated until fairly recently.

2.3.2 Data collation

Distribution data for *A. altissima* were collected from many sources and compiled into a global database and a South African database. Global distribution data were downloaded from (1) the Global Biodiversity Information Facility (GBIF); (2) Centre for Agriculture and Biosciences International (CABI); (3) the Global Invasive Species Database (GISD); and (4) Delivering Alien Invasive Species Inventories for Europe (DAISIE). Distribution data for South Africa were obtained from (1) the South African Plant Invaders Atlas (SAPIA) database (see Henderson 1998); (2) the City of Cape Town's Invasive Species Unit; (3) the South African National Biodiversity Institute's (SANBI) Invasive Species Programme (ISP); (4) herbarium records; and (5) from the online biodiversity website iSpot (http://www.ispotnature.org/). Additional data points were collected during random searches in the Western Cape, Gauteng and KwaZulu-Natal provinces during 2015. An article published in the popular South African magazine *Veld & Flora* (December 2015 issue) yielded 12 new occurrence records.

Since the environmental data were obtained from different data sources and at different levels of resolutions, both data sets were resampled at the same grid size to match the occurrence data for each scale (10-arc minute resolution for the global scale; 5-arc minute resolution for the national scale). Data were edited by removing replicates, records without any co-ordinates, obviously erroneous records (e.g. in the sea) and those that appeared to be outliers. This was done using the *biogeo* package available in R (Robertson et al. 2016).

Climatic variables were obtained from the WorldClim database (Hijmans et al. 2005). All 19 variables were downloaded at 10-minute spatial resolution for the global model, and at 5-minute spatial resolution for the South African model. When compared against each other (using a correlation test), we determined a high level of multicollinearity between the WorldClim climatic variables that were downloaded at both spatial scales. The utilization of environmental variables that exhibit high levels of multicollinearity is known to increase the appearance of errors in the final model output (Cruz-Cárdenas et al. 2014). Given the large number of climatic variables and the multi-collinearity among them, a principal component analysis (PCA) was performed at both spatial scales (Cabra-Rivas et al. 2016). For each of the first four axes (cumulative variation explained was >84%), variables accounting for the highest levels of variability were selected and used as climatic predictors. I selected the following climatic variables to account for variability at the global scale (in order of importance): mean temperature of the warmest quarter (Bio_10), temperature annual range (Bio_7), precipitation of the driest month (Bio_14), and mean temperature of the wettest quarter (Bio_8). At the national scale, the following climatic variables were selected: isothermality (Bio_3), temperature annual range (Bio_7), annual mean temperature (Bio_1) and precipitation of warmest quarter (Bio_18).

Land cover information was obtained from the GlobCover 2009 database for the global model (Arino et al. 2012), and from the 72 Class GTI South African National Land Cover Dataset (available at: http://bgis.sanbi.org/DEA_Landcover/project.asp) (DEA 2015) for the South African model. Categories were matched by grouping land-use data into six new categories for both the global and national models. I attempted to create similar land-use classes at both the global and national scales. However, since land-use data were from different sources, the final land-use classes differed slightly for the two spatial scales. For the global scale, I grouped the land-cover information from the GlobCover 2009 dataset into the following categories: (1) % built-up areas, (2) % agriculture, (3) % forest, (4) % mosaic vegetation, (5) % bare areas (no vegetation), and (6) % wetlands. These data were then aggregated to match a 10-minute spatial resolution. At the national scale, we categorized the land cover data as follows: (1) % human occupancy (urban and rural areas), (2) % agriculture, (3) % forest, (4) % mosaic vegetation, and (5) % bare areas (no vegetation). These data were then aggregated to match a 5-minute spatial resolution. All land-use classes at both spatial scales were used to develop species distribution models.

Human Footprint (HFP) data, which provides an index of anthropogenic impacts on the environment (Woolmer et al. 2008), were obtained from the SEDAC database (Sanderson et al. 2002) for both the global and country models. These data were then aggregated to match a 10-minute spatial resolution for the global scale, and a 5-minute spatial resolution for the national scale. HFP is a global dataset of 1-km grid cells created from nine global data layers that include human population pressure, human land use and infrastructure and human access. It indicates the degree of disturbance in the community ranging from 0 (wild) to 100 (highly disturbed) (Woolmer et al. 2008). For each model, the final set of explanatory variables included climatic, land use and human footprint variables (Table 2.1).

2.3.3 Modelling at a global scale

A set of ensemble models were built to characterize the full-range niche requirements for *A. altissima* at a global scale. A total of 3205 unique global occurrences for *A. altissima* encompassing both the native and non-native ranges of the species were used. The choice of algorithm influences the overall model output (Thuiller et al. 2004; Roura-Pascual et al. 2009; Cabra-Rivas et al. 2016). However, there is no single technique that is most affective at predicting potential species distribution (Pearson et al. 2006). Consequently, four algorithms were selected to model the potential global distribution of *A. altissima*. Two regression methods - Generalized Linear Models (GLM; Faraway 2016) and Multivariate Adaptive Regression Splines (MARS; Friedman 1991) - and two machine-learning methods- Random Forest (RF; Liaw and Wiener 2002) and Generalized Boosted Models (GBM; Ridgeway 1999) - were selected. All algorithms were implemented using the *biomod2* package (Thuiller et al. 2013) in R. All of the selected algorithms require presence-absence data to build models (Elith and Leathwick 2009), my global dataset included presence-only records. Barbet-Massin et al. (2012) found that models fitted with a large number of pseudo-absences that are equally weighted to the presences (i.e. weighted sum of pseudo-absences equals the weighted sum of presences) produced the most accurate predicted distribution models. They also found that fewer replicates were required when a larger number of pseudo-absence records were generated. Therefore, a single set of 10000 pseudo-absence records was generated (Barbet-Massin et al. 2012). To account for the geographical bias associated with my presence data, I restricted the selection of pseudo-absence points to the grid cells surrounding every presence (no further than four grid cells distance away from each presence) (Barbet-Massin et al. 2012). I thereby minimized commission errors in areas that may be suitable for the species but are not yet colonized

(Cabra-Rivas et al. 2016). I implemented a split-sample cross-validation procedure where all models were calibrated on 70% of the initial data randomly selected, and evaluated on the remaining 30% (70-30 % split) with the area under the ROC curve (AUC; Fielding and Bell 1997; Cabra-Rivas et al. 2016). Ten cross validations were performed for each algorithm and pseudo-absence dataset resulting in a total of 40 different models being calculated for the species globally (one pseudo-absence dataset × four algorithms × ten replications). To improve the overall accuracy of SDM predictions, only models with an AUC score ≥ 0.8 were retained to build a committee averaging ensemble model (Crossman and Bass 2008). A single output consisting of the percentage of agreement among models is created by utilizing this method (Gallien et al. 2012).

2.3.4 Modelling at a country scale

Presence records for *A. altissima* in South Africa were pooled from various databases and sources. Replicates and unreliable records were removed from the dataset using *biogeo* with a single record being retained for each 5-minute grid cell. This left a total of 539 unique records. However, to ensure that testing took place on spatially separated blocks, I set a minimum distance of 30 km between each presence record, thereby avoiding biases associated with over sampling in certain areas and ensuring the accuracy of the final model output. This further reduced the total number of unique records to 90. Pseudo-absences were selected in a way that both minimized the sampling biases from the occurrence data (Phillips et al. 2009) and accounted for the disequilibrium of the species in South Africa (Gallien et al. 2012). I selected pseudo-absences within the vicinity of any of the presence records (no more than four grid cells distance from each presence record) so that they more likely reflected unsuitable habitat than dispersal limitations (Cabra-Rivas et al. 2016). I used the predictions of the global models to attribute weights to our pseudo-absences as a way of avoiding contingent absences. Weights ranged from 0 (low probability of being a true absence) to 1 (high probability of being a true absence) (for further details see Gallien et al. 2012). 1836 pseudo-absence records were selected to represent all areas surrounding each presence records. As with the global model, I used the same four statistical algorithms followed by 10 cross-validation repetitions resulting in a total of 40 models being calculated for the species in South Africa (one pseudo-absence dataset × four algorithms × ten replications). The same split-sample cross-validation procedure was used as in the global model (70-30%). To avoid a false inflation of AUC measures due to spatial autocorrelation, a filtering point approach was selected (Marcer et al. 2012). A filtering point approach sets a minimum spatial and environmental distance between occurrences and examines these for residual autocorrelation (Marcer et al. 2012). The smaller number of species occurrences together with the high restrictions imposed on pseudo-absence selection lead to a decrease in AUC scores (Lobo et al. 2008). As such, only models with AUC scores ≥ 0.7 were retained to build the committee averaging ensemble model.

2.3.5 Statistical analyses

The relative importance of each of the selected variables was determined at both spatial scales. A confusion matrix was produced showing: 1) the number of points predicted as suitable by both the global and national models; 2) the number of points predicted as suitable by either the global or the national models; and 3) the number of points predicted as unsuitable by both the global and national models (Fig. 2.4) (Fielding and Bell 1997). Using the values obtained from the confusion matrix, the true skill statistic (TSS) as well as the sensitivity and specificity values were calculated (Fielding and Bell 1997; Allouche et al. 2006). Sensitivity refers to the proportion of correctly predicted presences whereas specificity refers to the proportion of correctly predicted absences (Allouche et al. 2006). TSS is used to measure the performance of models that generate presence-absence predictions, however unlike the popular Kappa statistic, TSS is independent of prevalence (Allouche et al. 2006).

2.4 Results

Table 2.1 Final set of explanatory variables specifying the scale and data source used to develop the species distribution models at the global and national scale.

Variable type	Variable description	Scale	Data source
Climate	Precipitation of driest month [bio14]	Global	WorldClim database (Hijmans et al. 2005; http://www.worldclim.org/bioclim.htm) [Accessed in
Climate	Mean temperature of warmest quarter	Global	*A
Climate	Mean temperature of wettest quarter	Global	*A
Climate	Temperature annual range [bio5-bio6]	Global, country	*A
Climate	Precipitation of warmest quarter	Country	*A
Climate	Isothermality [bio2/bio7] [*100]	Country	*A
Climate	Annual mean temperature [bio1]	Country	*A
Land use	% Agriculture	Global	GlobCover 2009 dataset (Arino et al. 2012; http://due.esrin.esa.int/page_globcover.php)
Land use	% Bare areas	Global	*B
Land use	% Built-up areas	Global	*B
Land use	% Forests	Global	*B
Land use	% Mosaic vegetation	Global	*B
Land use	% Wetland	Global	*B
Land use	% Human occupancy (urban and rural	Country	72 Class GTI South African National Land Cover Dataset (DEA Open Access, 2015;
Land use	% Wetland	Country	*C
Land use	% Forest	Country	*C
Land use	% Agriculture	Country	*C
Land use	% Mosaic vegetation	Country	*C
Land use	% Bare areas	Country	*C
Disturbance	Human footprint	Global, country	SEDAC database (Sanderson et al. 2002; http://sedac.ciesin.columbia.edu/data/set/wildareas-

2.4.1 Relative importance of distribution drivers

Cumulatively, climate variables (62.2%) were the most influential drivers affecting the distribution of *A. altissima* at the global scale. This was followed by land use (24.9%) and human-mediated disturbances (14.6%). In contrast, at the country scale human-mediated disturbance (65.6%) was the most influential driver, followed by land use (12.9%) and then climate (21.8%) (Fig. 2.1a).

Individually, mean temperature of the warmest quarter (26.6%) and temperature annual range (19.9%) were the most influential variables at the global scale; followed by the percentage of built-up areas (16.2%) and human-mediated disturbances (14.6%) (Fig. 2.1b). At the country scale, human-mediated disturbances (49.8%) were the most influential variables affecting the distribution of *A. altissima,* followed by the land use category - percentage human occupancy (21.9%). Isothermality (mean diurnal range/temperature annual range) (7.3%) and temperature annual range (4.9%) were the two most influential climatic variables at the country-level scale (Fig. 2.1c).

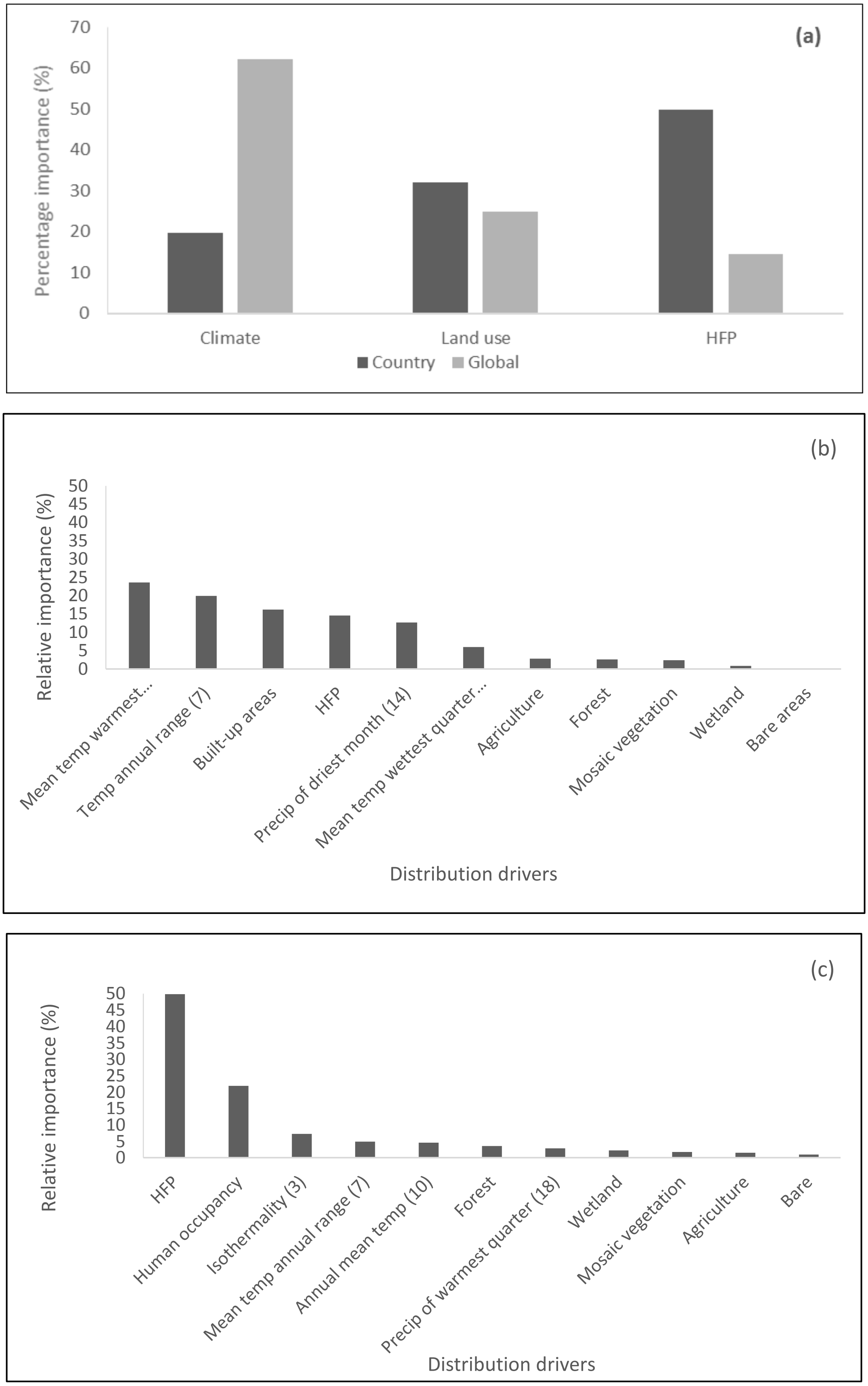


Figure 2.1: Relative importance of the variables that could predict the distribution of *A. altissima* cumulatively at both global and country-level scales (**a**); and individually at the global scale (**b**) and the country-level scale (**c**).

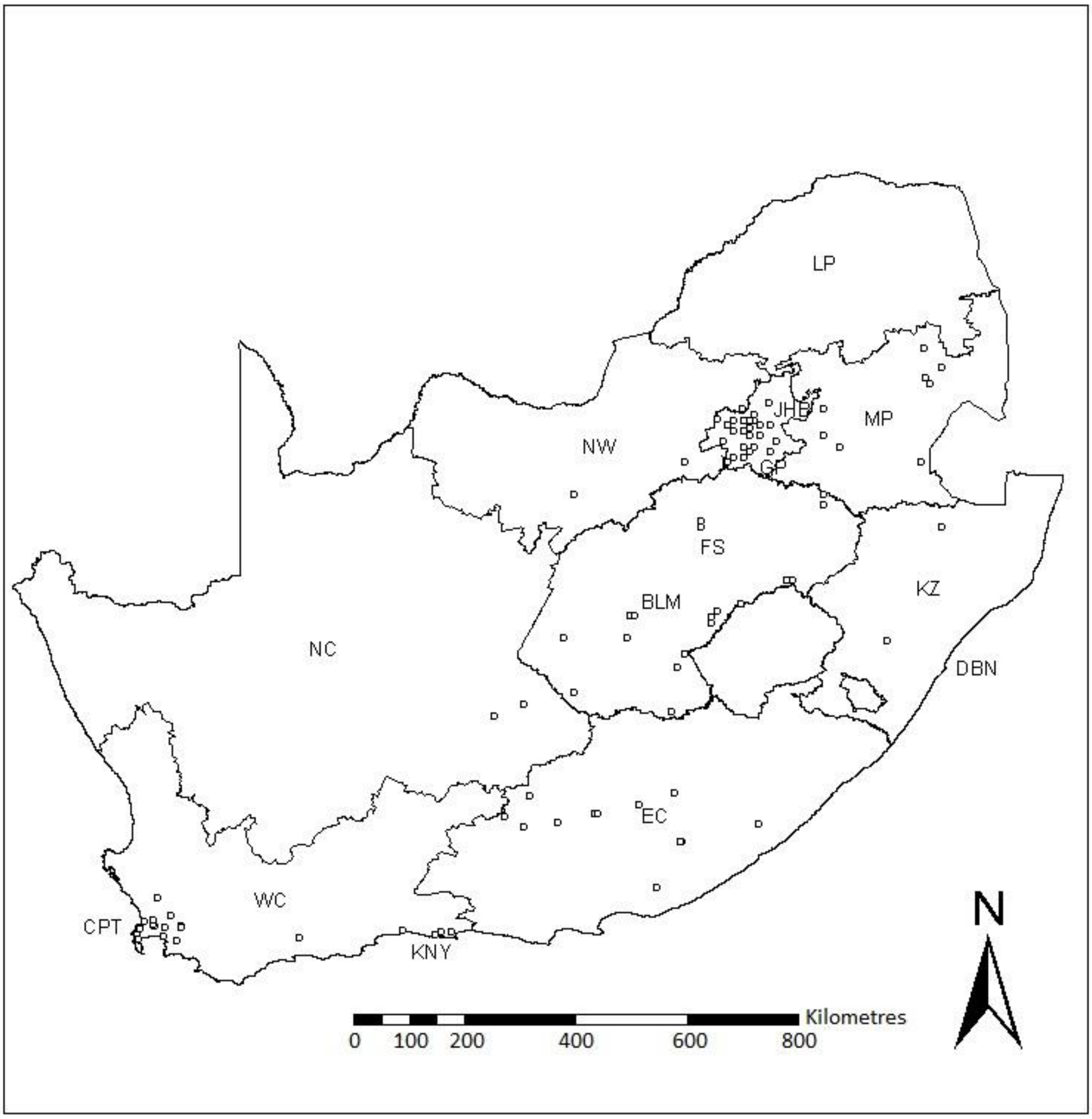


Figure 2.2: Current distribution of *Ailanthus altissima* in South Africa. All provinces (WC = Western Cape; EC = Eastern Cape; KZ = KwaZulu-Natal; MP = Mpumalanga; LP = Limpopo; GP = Gauteng; FS = Free State; NW = North West; NC = Northern Cape) and selected cities (CPT = Cape Town; KNY = Knysna; DBN = Durban; JHB = Johannesburg; BLM = Bloemfontein) are shown.

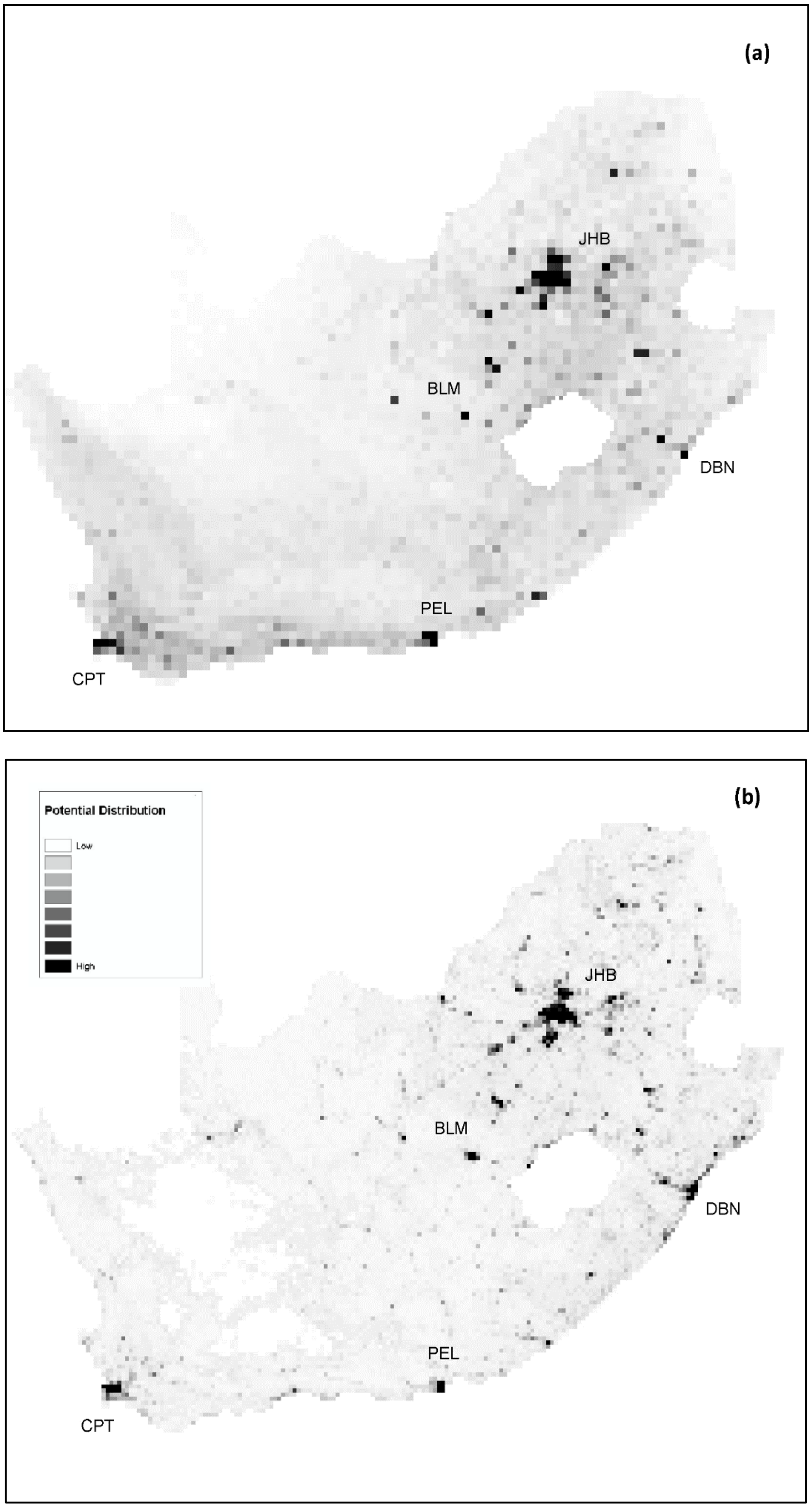


Figure 2.3: Maps showing areas predicted suitable for *Ailanthus altissima* in South Africa in global-scale (**a**) and country-scale models (**b**). Areas identified as being highly suitable are shown in black; unsuitable areas are shaded grey. Cities in which *A. altissima* is abundant (CPT = Cape Town; PEL = Port Elizabeth; DBN = Durban; JHB = Johannesburg; BLM = Bloemfontein) are shown in both figures.

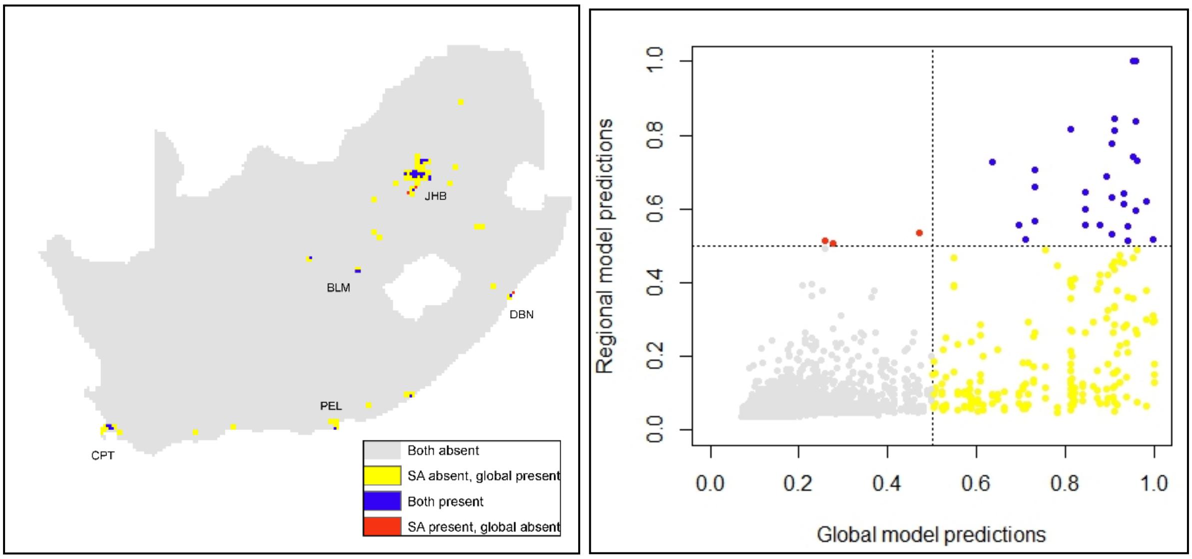


Figure 2.4: Combined model output and confusion matrix showing areas predicted to be suitable by both the global- and national models (*blue*), areas that are predicted as suitable by just the global model (*yellow*) or national model (*red*) and areas that are predicted as unsuitable by both the global- and national models (*grey*).

2.4.2 Degree to which *A. altissima* has expanded its potential range, and risk maps

Within South Africa, *A. altissima* is widespread and abundant throughout the province of Gauteng (Fig. 2.3). Projections from both the global and national models predicted presences in most grid cells occurring throughout this province. The species is fairly widespread in the southwestern part of the Western Cape, especially in and around the cities of Cape Town and Knysna. The species has a scattered distribution throughout parts of the Eastern Cape, Free State and Mpumalanga. Both the global and national models predicted presences in grid cells that include the cities of Port Elizabeth and East London (east of Port Elizabeth) as well as Bloemfontein. Global model projections predicted presences in two grid cells in Mpumalanga and the Free State. The species is rare in the KwaZulu-Natal, North West and Northern Cape provinces, with two isolated populations occurring in each province. The national- and global-scale models separately predicted presences in grid cells surrounding Durban which currently have no records of *A. altissima* occurrence (Fig. 2.4). The global model predicted suitable grid cells in the North West province but these coincide with areas that already have a record of *A. altissima* occurrence. Both the global- and national-scale models predicted absences in the Northern Cape. Throughout South Africa, both the current and potential distribution of *A. altissima* appear to coincide largely with urban areas.

The confusion matrix shows that a total of 29 grid cells were predicted to be suitable for the species in both the global- and national models; 149 points were predicted to be suitable by only the global-scale model; 3 points were predicted to be suitable by only the national model; and 16131 points were predicted as being unsuitable by both models. I determined the sensitivity (*Sn* = 0.91) and specificity (*Sp* = 0.99) values and the TSS value (TSS = 0.90).

2.5 Discussion

2.5.1 Relative importance of predictor variables

The potential distribution of invasive species is influenced by many factors whose relative importance varies according to spatial scale (Rouget and Richardson 2003; Guisan and Thuiller 2005; McGill 2010; Cabra-Rivas et al. 2016). Factors such as climate (Hijmans and Graham 2006; Hellman et al. 2008), land use (McKinney 2008) and anthropogenic effects (Hulme 2009) are well known to have an effect on the distribution of invasive species globally. This study (and others; see Guisan and Thuiller 2005; Gallien et al. 2010; Cabra-Rivas et al. 2016) highlights the importance of incorporating these multiple factors into models to determine the potential range of an invasive species. My analysis showed that climatic factors were most important for explaining range limits at the global scale (Vicente et al. 2010; Cabra-Rivas et al. 2016). This agrees with several other studies that have concluded that, at a global scale, climate has the greatest effect on the broad range limits of invasive species (see Hellman et al. 2008; Jeschke and Strayer 2008). This was followed by land use and then human-mediated disturbance. A different trend was observed at the national scale, with human-mediated disturbance being the most influential driver affecting the distribution of *A. altissima* in South Africa. The current distribution of the species in South Africa coincides with large cities and towns, suggesting that the historical planting of the species occurred within urban and suburban areas. *Ailanthus altissima* has spread throughout its adventive range due to its introduction as a popular urban ornamental plant (Kowarik and Säumel 2007); for this reason, the species is most common and abundant in cities and towns. The first record of *A. altissima* in South Africa is from Cape Town in 1834 (Bradlow 1965), but very little is known about the subsequent history of dissemination of the species throughout the country. Female trees were clearly selected for cultivation in urban areas in preference to male trees because the flowers of male trees emit a foul-smelling odour. The regeneration biology of the species in South Africa has not been studied, but it is likely that the preference of female trees in plantings has reduced seed production and that regeneration has been largely through vegetative means which has slowed the spread. It is likely that the species will spread and become increasingly abundant throughout current areas of establishment (i.e. urban and suburban areas of South Africa). Land use and climate did not have as great of an influence as human mediated disturbances at the country scale.

2.5.2 Relevant determinants of species distribution

Four climatic variables account for the highest degree of variability at both spatial scales. The climatic variables that were selected (see Table2.1) encompass a broad range of climatic conditions and were thus ideal for modelling the distribution of *A. altissima*. Although *A. altissima* tolerates a wide range of climatic conditions, it is most common and abundant in temperate climatic zones (Knapp and Canham 2000; Kowarik and Säumel 2007; Clark et al. 2014). The climatic variables that were identified as key drivers were consistent with the climatic requirements reported in the literature (see Kowarik and Säumel 2007). In agreement with the findings of Cabra-Rivas et al. (2016) I found that at the global scale, the distribution of *A. altissima* was strongly influenced by intermediate temperature conditions. Warm temperatures during the day (21°C - 27°C) that drop slightly at night (13°C - 18°C) characterize intermediate temperature conditions (Shaver et al. 2000). Extreme fluctuations rarely occur in areas with intermediate temperature conditions. Cabra-Rivas et al. (2016) found annual mean temperature to be the most influential distribution driver at the global scale (35.3%) whereas I found mean temperature of the warmest quarter to be the most influential variable (26.6%). Although these variables do differ, a correlation test between the two suggests that they are highly correlated and thus interdependent. These results are to be expected as the species is exposed to similar conditions in its native range (Albright et al. 2010). Precipitation also influenced the distribution of the species at the global scale because, although largely drought-tolerant, *A. altissima* does not grow well in areas with pronounced droughts (Albright et al. 2010). Similar results were obtained at the national scale with intermediate climatic conditions relating to isothermality (mean diurnal range/temperature annual) and annual range in temperature.

I previously highlighted the importance of human-mediated disturbances over other determinants of distribution at the national scale, but it is important to note that at both the global and national scales I found the percentage of built-up areas (global), percentage of human occupied areas (country-level) and zones with high levels of human-mediated disturbance (human footprint indicator) (both spatial scales) to have a large influence on the distribution of *A. altissima*. The spread of this species has been facilitated by its dissemination globally as a popular ornamental plant (Kowarik and Säumel 2007). A high level of human influence is linked to high propagule pressure (Cabra-Rivas et al. 2016) which has likely facilitated the spread and establishment of this species in its adventive range. This high human footprint (human mediated disturbances) in conjunction with the anthropogenic influences that are characteristic with various transportation pathways and dispersal corridors within built-up areas have clearly acted as efficient mechanisms for promoting the spread of *A. altissima* throughout urban ecosystems in South Africa. This agrees with findings from other parts of the world where *A. altissima* is most common and abundant in urban areas (Huebner 2003). It is therefore to be expected that human influence would have a large effect on the distribution of this species in South Africa.

In summary, I can conclude that the intermediate climatic conditions have a large effect on shaping the distribution of *A. altissima* at both global and national scales. These, together with high levels of human-mediated disturbance in built-up areas, ensure rapid rates of proliferation.

2.5.3 Degree to which the potential range has been occupied, and risk maps

Most areas identified as being suitable for *A. altissima* occurrence in South Africa already have established populations; this suggests that further wide-scale spread throughout currently uninvaded areas in the country is unlikely. Although substantial range changes of the species in South Africa under current environmental conditions are unlikely, increases in population density, due to the high rates of seed production (Kowarik and Säumel 2007), are very likely. The species showed a high degree of prevalence in areas that are heavily affected by human activities (urban and suburban areas). This suggests that in the absence of management, population density will increase in and around areas where the species is already established (i.e. in cities and in towns).

Although the global and national models are largely in agreement (number of grid cells where presences were predicted by both the global and national model = 29; number of grid cells where absences were predicted by both models = 16131), there are certain areas that are identified as suitable only by either the global (number of grid cells where presences were predicted by only the global model = 149) or national models (number of grid cells where presences were predicted by only the country model = 3). There are several possible reasons for this. Firstly, the reason for some areas being identified as suitable in the global model but not in the country-level model could be the result of the coarseness of the environmental variables that were used (Guisan et al. 2007). Although not completely inaccurate, the use of coarse-grain variables could increase the potential error that may arise when downscaling the study area from global to national scale (Graham et al. 2007, Guisan et al. 2007) as was done in this study for South Africa. Reasons for areas being identified as suitable for the species in the national models but not in global models could include: (1) the presence of locally-adapted *A. altissima* populations; (2) interspecific competition with other plant species; or (3) more favourable levels of disturbance within the environment in which it has been introduced (Cabra-Rivas et al. 2016). The most likely explanation however is that the species is an emerging invader, and has only recently entered the phase of rapid population growth. All possibilities are plausible, and the true causes of such inconsistencies are unknown.

My model comparison yielded a higher specificity value (*Sp* = 0.99) in comparison to the sensitivity value (*Sn* = 0.90). This suggests that my projected model outputs were largely in agreement about where both absences (99%) and presences (90%) were depicted. Most of South Africa is not suitable for invasion by *A. altissima*, so this high specificity value does make sense. All grid cells in which presences were predicted by either the global or national model are close together (i.e. global model output = country model output) proving that the models at both spatial scales were not only in agreement about predicted absences, but also regarding predicted presences. A high TSS value (TSS = 0.91) further indicates that our models were in agreement and that our predictions were accurate (Allouche et al. 2006).

When used together, habitat suitability and range-filling analyses are useful tools as they enable stakeholders and managers to identify areas where early detection, rapid response (EDRR) initiatives and urgent eradication, containment and control efforts should be implemented (Cabra-Rivas et al. 2016). Containment and reducing the size of established *A. altissima* populations nationally will limit further environmental and human degradation that may result from population density increases and spread (Wilson et al. 2007). EDRR initiatives in areas with low densities of *A. altissima* will improve the possibility of species eradication with follow-up control measures preventing future re-establishment of the species. Similar results were observed on *Acacia stricta* (see Kaplan et al. 2014).

2.6 Conclusions

Effective management of invasive species requires the accurate assessment of the potential geographical range of the invaders and an understanding of the factors that promote their spread. This study indicates that although *A. altissima* can spread further in South Africa, wide-scale spread throughout the country highly unlikely, given the species' preference for urban conditions. Delimiting potential areas of invasion in relation to current areas of establishment ultimately reduces management costs. I identified distinct differences in the model outputs that were achieved at both the global and national scale with climate being the prevailing factor influencing the spread of the species globally, and human mediated disturbances being the most influential driver at the national scale. This study highlights the importance of incorporating different environmental variables at various spatial scales to identify areas of high invasion potential. This multi-scale approach facilitates the early detection of invaders ultimately preventing their spread and introduction into high risk areas.

Acknowledgements

This project was jointly funded by BTA Pipe Supplies and the DST-NRF Centre of Excellence for Invasion Biology. DMR acknowledges funding from the DST-NRF Centre of Excellence for Invasion Biology and the National Research Foundation of South Africa (grant 85417). We thank many staff members from the City of Cape Town's Environmental Resource Management Department (ERMD) and the Invasive Species Unit of the South African National Biodiversity Institute who provided support and field-work assistance during this study.

CHAPTER 3: *AILANTHUS ALTISSIMA* (SIMAROUBACEAE; TREE OF HEAVEN) IN THE CITY OF CAPE TOWN, SOUTH AFRICA: WHERE IS IT? WHERE COULD IT BE? WHAT CAN BE DONE ABOUT IT?

Target journal for publication: Landscape and Urban Planning

3.1 Abstract

The constant flow of goods into and out of cities has resulted in the proliferation of invasive species in urban areas, and cities are viewed as 'hotspots' for invasive species. Conditions that have been altered due to human activities enable some alien species to proliferate rapidly throughout urban centres, often also spreading into natural and semi-natural areas that occur at the urban/wildland interface. Evaluating patterns of distribution in terms of ecological and biogeographical species preferences gives managers a better understanding of the invasion process and options for management. Identification of invasion 'hotspots' for a particular species using GIS and remote sensing techniques helps to focus resources where they would most be needed ultimately saving money and time. This study focussed on *Ailanthus altissima* – an emerging invasive tree species in Cape Town. Using geographic information system (GIS) techniques I evaluated the distribution of the species in Cape Town and identified potentially invasible areas. We found that throughout Cape Town, *A. altissima* occupies relatively high-income suburbs with podzolic soils that receive high rainfall. From these findings, I predicted that the species has the capacity for substantial further spread in the city. Using the suburb of Newlands as a case study I evaluated the population structure of *A. altissima* at a fine scale with the aim of developing a management protocol and costing scheme that could be used by city managers to control not only this species but other emerging urban invaders. We found that eradication could be a cost-effective option in Newlands. The approach applied in this study could be used for other emerging urban invaders to improve the effectivity of management initiatives.

Keywords

Biological invasions; costing schemes; distribution patterns; spatial analysis; tree invasions; urban invasions

3.2 Introduction

Invasive alien species (IAS) are organisms that have been introduced to new regions through human actions and that have spread from sites of introduction (Richardson et al. 2000). The rise of global trade and long distance transportation has led to an increase in the number of human mediated introductions globally (Lockwood et al. 2013) and as such, cities have become a hotspot for invasive species (Gaertner et al. 2016). *Ailanthus altissima* (Simaroubaceae; tree of heaven) is an example of a species that has become a prolific invader in urban ecosystems throughout the world (Kowarik and Säumel 2007). The species, native to China, has spread throughout its adventive range due to its introduction as a popular ornamental tree in urban centres (Burch and Zedaker 2003). Although a notorious invader in the northern hemisphere (Kowarik and Säumel 2007), *A. altissima* is yet to replicate similar levels of invasion success in South Africa (Walker et al., under review). Several factors facilitate the spread of invasive species in urban ecosystems; these include a high level of human influence and exposure to many micro-climatic conditions (Gaertner et al. 2016). Understanding these factors by evaluating the distribution patterns of a species will enhance management of invasive species in urban ecosystems. In this regard, it has become particularly useful to evaluate the biology and ecology of a species focussing specifically on what makes the species a successful invader in other countries, and to use this information to better understand the invasive potential of the same species in South Africa.

3.2.1 Invasive species in cities – spread and distribution

The Import and export of goods into and out of cities has resulted in the proliferation of IAS in urban areas (Kowarik 2011) with transport linkages facilitating the introduction and spread of non-native species through diverse dispersal pathways (Dehnen-Schmutz et al. 2007). Non-native organisms are exposed to habitats, soils, and climatic and hydrological conditions that have been altered through human activities (Gaertner et al. 2016). If species are pre-adapted to conditions similar to those that exist in their native range, they may undergo rapid proliferation following introduction to new areas (Pickett et al. 2001; Kowarik 2011). Ornamental invasive plant species found in gardens often propagate rapidly, spreading throughout urban ecosystems and displacing the indigenous flora (Alston and Richardson 2006; Foxcroft et al. 2008). Damage to human infrastructure, which involves the weakening of the structural integrity of the building, is also common (*Ailanthus altissima*, for example) (Kowarik and Säumel 2007). This forms part of a multitude of problems associated with urban invasive species and is only one of the many problems that are associated with urban invasive species (see van Wilgen and Scott 2001 and Gaertner et al. 2016 for other examples). Another problem with introduced plants occurring in cities is that they often spread into adjoining natural and semi-natural areas (Alston and Richardson 2006; Bowers et al. 2006). The wildland/urban interface in many areas is threatened by a variety of 'edge effects' and is especially vulnerable to invasion by introduced plants that spread from suburban gardens (Alston and Richardson 2006). This case has been particularly prevalent with introduced plants in Cape Town, South Africa.

3.2.2 The problem of invasions in the city of Cape Town

The city of Cape Town (hereinafter referred to as 'the city') is in the heart of the Cape Floristic Region, an area with exceptionally high levels of plant endemism (Cowling et al. 1996) and which is recognised as a global biodiversity hotspot (Myers et al. 2000). A variety of nature reserves and biodiversity networks occur within the boundaries of the city, the most notable of these being Table Mountain National Park (Gaertner et al. 2016). Cape Town currently has a population of around 3.8 million people that is growing by an estimated 2.57 % per annum (Statistics South Africa, 2011). Ongoing increases in the city's population size have resulted in an increase in the trade of ornamental plants within the city (van Wilgen 2012). Many of these introductions remain undetected and/or unregulated which leads to a growing 'invasion debt' of species that have been introduced in parts of the city but which have yet to express the full extent of their invasiveness (Rouget et al. 2015). Understanding the full extent of a species' invasiveness as well as its invasion potential are central to the success of invasive species management and control efforts (Hauser and McCarthy 2009).

3.2.3 Managing invasions in cities

The South African Department of Environmental Affairs is responsible for the administration of the National Environmental Management: Biodiversity Act (NEMBA). This legislation places obligations upon all landowners with respect to the effective management of invasive species (Gaertner et al. 2016), including the residents of Cape Town (Gaertner et al.

2016). To assist with NEMBA, the city established an Invasive Species Management Unit (ISMU) in 2008 (Gaertner et al. 2016). Among other things, the ISMU manages an early detection and rapid response (EDRR) program. Management of IAS is most effective at the early stages of invasion, before the species are well-established and widespread in a particular environment (Simpson et al. 2009; Simberloff et al. 2013). The EDRR program targets emerging invaders with relatively localised populations that have not surpassed a point where containment and eradication are potentially possible (Wilson et al. 2013). A total of 15 plant species (including *Ailanthus altissima*) are currently targeted by the EDRR unit which relies heavily on public involvement for reporting sightings of species across the city.

3.2.4 Species distribution

Although the EDRR unit's approach has shown levels of success, both ecologically (providing a viable means of controlling IAS) and economically (cheaper), the accurate determination of the full extent (distribution) of IAS throughout the city is problematic. Inaccessibility to private land and the large area that must be surveyed are key challenges. Eradication is a priority objective for EDRR programmes worldwide (Myers et al. 2000), but not knowing the full extent of the distribution of an IAS greatly reduces the chances of achieving eradication. The use of remote sensing (RS) and geographic information system (GIS) techniques have improved IAS inventories, enabling stakeholders and managers to establish the full extent of an invasive species' distribution in particular environments. Evaluating patterns of distribution in terms of ecological and biogeographical species preferences enables managers to gain an understanding of the processes that make a species a successful invader (Kinlan and Gaines 2003; Sax et al. 2005). Using the knowledge of a particular species' preferences along with the evaluation of areas that are probable invasion 'hotspots' for a species using GIS techniques helps to delimit areas of unlikely invasion potential, ultimately saving money and time (Joshi et al. 2004). The development of risk maps has become a useful tool when it comes to highlighting potential invasion hotspots and delimiting areas of unlikely invasion potential (Hulme 2009), and the use of these has been well documented particularly in the field of invasion biology (see Leung et al. 2002; Andersen et al. 2004; Jiménez-Valverde et al. 2011).

In this study, I evaluate the distribution pattern of *Ailanthus altissima* – an EDRR target species in the City of Cape Town - and determine potential options for management. In particular, I address the following questions: 1) What is the current distribution of *A. altissima* in the City of Cape Town?; 2) Are there clear ecological and biogeographical preferences (in terms of soil, land use, rainfall and socio-economic differences) that have had an influence on the distribution of the species?; 3) Which areas are potential invasion hotspots for *A. altissima* invasion in the future? and 4) Using the suburb of Newlands as a case study, what would be the best approach to managing *A. altissima* in the city? The outcome of the study will be to provide guidelines or a protocol for managing an emerging invader in an urban area. It will provide managers with guidelines on how to determine the distribution of a species in an urban environment and to utilise this information to determine the feasibility of eradication.

3.3 Methods

3.3.1 Study species

Ailanthus altissima Mill. Swingle (Simaroubaceae; tree of heaven) is a deciduous, dioecious tree species that is native to China. The species has spread throughout its non-native range due to its widespread dissemination as an ornamental plant (Kowarik and Säumel 2007; Constán-Nava et al. 2010). To date, *A. altissima* is established on all continents except Antarctica. In its adventive range *A. altissima* is most common and abundant in urban areas where it mainly occurs on disturbed sites, in degraded fields, along roads, and in riparian habitats (Kowarik and Säumel 2007; Constán-Nava et al. 2010). The species has several characteristics that make it a successful invader of urban environments, including prolific seed production (ca. 350 000 per female tree/year), rapid juvenile growth (Burch and Zedaker 2003), the ability to withstand harsh environmental conditions, including high levels of atmospheric pollution (Lawrence et al. 1991), and the capacity to reproduce vegetatively after disturbance (Bory et al. 1991; Kowarik 1995; Kowarik and Säumel 2007; Constán-Nava et al. 2010). *Ailanthus altissima* grows in a variety of soil types that are exposed to varying levels of annual precipitation (Kowarik and Säumel 2007). Morphological plasticity, combined with physiological adaptations (see Kowarik and Säumel 2007) have enabled the species to survive in environments that are exposed to a variety of abiotic conditions. Although the species is not a recent introduction to South Africa (Henderson 2006), *A.*

altissima is yet to replicate similar levels of invasion success that have been achieved in several northern hemisphere countries (Kowarik and Säumel 2007). If the species is not correctly managed, its potential for density and abundance increases in several parts of the country (see Chapters 1 & 2).

3.3.2 Data collation

Distribution data for *A. altissima* in Cape Town were obtained from various sources including: 1) the City of Cape Town's Invasive Species Management Unit; 2) the South African National Biodiversity Institute's (SANBI) Invasive Species Programme (ISP); 3) the South African Plant Invaders Atlas (SAPIA) database (see Henderson 1998); and 4) the online biodiversity website iSpot (http://www.ispotnature.org/). Additional points were collected during random searches between April 2015 and May 2016. These random searches normally took place during personal drives between and within cities and towns. Whenever the species was located, its location was logged using a handheld GPS device. Information leaflets were distributed to residents throughout the City of Cape Town to encourage them to report sightings of *A. altissima*. Articles were also published in the popular national botanical magazine *Veld & Flora* (December 2015 issue) and in the Western Cape newspaper *Cape Argus* (April 2015); these articles yielded 24 new occurrence records. All points were cross-checked and validated to ensure accuracy and 236 occurrence points were then compiled into a single 'City of Cape Town' database.

3.3.3 Spatial analysis

We evaluated, using GIS techniques, the distribution of *A. altissima* throughout the city in terms of the number of plants per 1) soil type; 2) land-use type; 3) rainfall zone; and 4) income class. Soil and land use data (which subdivided the area of the city into urban, agricultural and natural vegetation) were accessed from the City of Cape Town's open data portal (https://web1.capetown.gov.za/web1/OpenDataPortal/AllDatasets), and rainfall data were received from the Centre for Geographical Analysis (CGA) at Stellenbosch University. Income classes were determined on a per-polygon basis using the Living Standard Measurement (LSM) threshold which serves as a segmenting tool that disregards race, gender, age or any other variable used to categorise people, and instead groups people according to their living standards (Grosh et al. 2000). LSM values are ranked from ten (highest) to one (lowest) (Grosh et al. 2000). This information was also received from the CGA who previously utilised LSM thresholds to class the average income per polygon throughout South Africa. Using this concept, all urban areas in the city were classified into high, medium, and low income areas. A risk map was then created using all the above-mentioned data (soil, land use, rainfall and income) to identify areas that are potentially susceptible to invasion by *A. altissima*. To do this, individual layers were created into areas of high and low risk for each of the variables. All layers were then merged together]to produce one consolidated map indicating high (scored as 1) and low (scored as 0) suitability.

3.3.4 Case study: Newlands

Because it was not possible to develop an accurate management protocol for the entire city (due to a spatial bias in the occurrence data acquired as well as the large area that would need to be actively sampled), I focussed on one suburb: Newlands. Newlands is a high-income suburb situated at the foot of Table Mountain (Turok 2001) with an estimated population of 1500 people/km^2 (Census, 2011). Various roadways and footpaths, together with high rainfall density, numerous drainage channels and the Liesbeek River that meanders through the suburb (Wilkinson, 2000), provide a variety of dispersal pathways for the spread and proliferation of invasive plant species in Newlands. Furthermore, the proximity of the residential portion of Newlands to the Newlands Forest (which constitutes a section of the Table Mountain National Park), and the high number of *A. altissima* records, makes this suburb an ideal case study. I systematically sampled each road (approximately 200 kilometres in total) in Newlands between February and May 2016, and recorded the co-ordinates for the occurrence of all *A. altissima* individuals found throughout the suburb. Additional information which included whether the plant was mature or not as well as the estimated height of each plant were also recorded.

I set out to roughly determine the cost of eradication for *A. altissima* in Newlands. Various tree felling companies throughout the city were contacted as a means of verifying this. i provided these companies with the information collected during my systematic road searches (in other words, maturity and plant size) as a means of obtaining an accurate quotation for the eradication and removal of individual plants. The price of herbicides and associated applicators were established online and, together with the quotes that were received from the tree felling companies, I determined the average cost for controlling *A. altissima* in Newlands.

3.4 Results

3.4.1 Spatial analysis

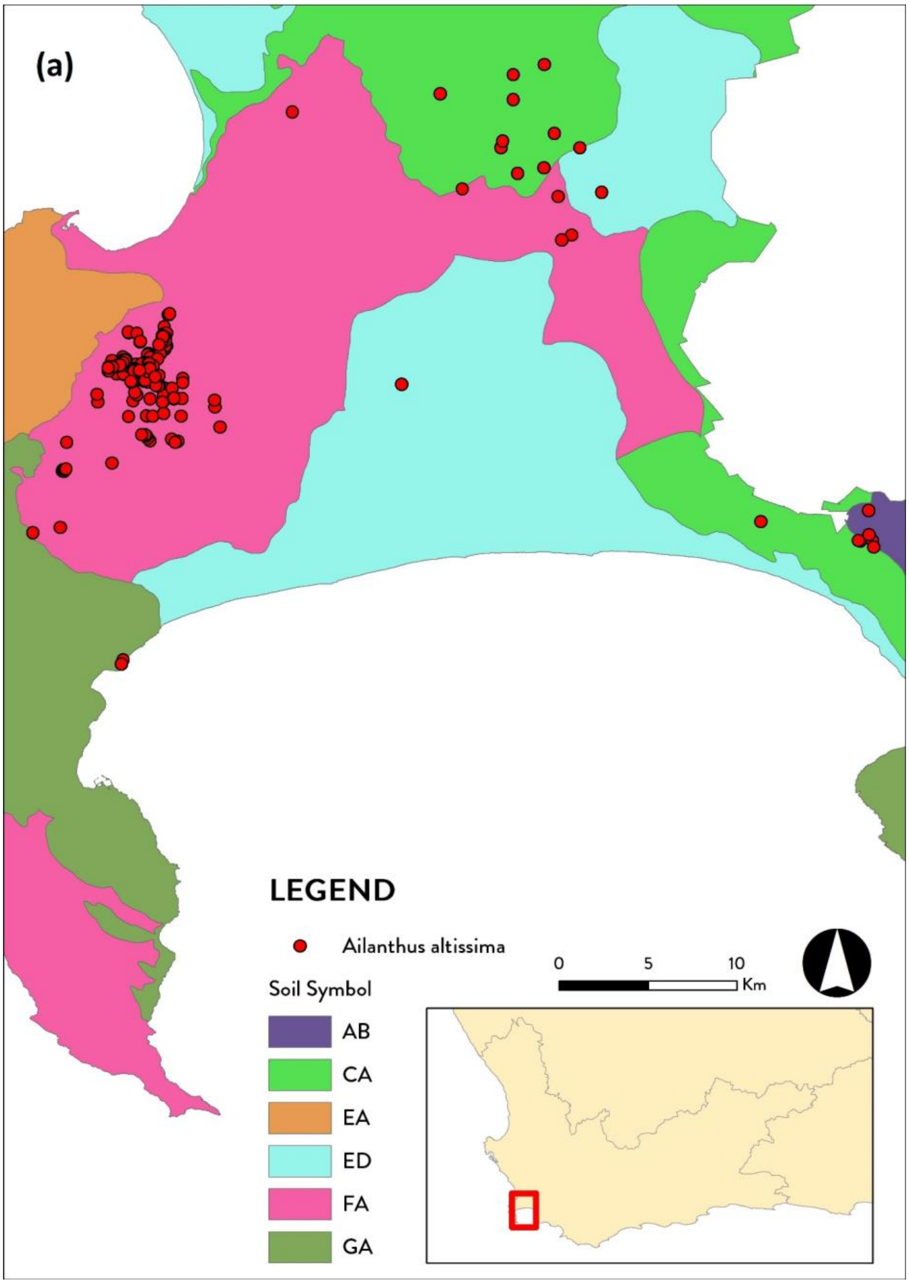


Figure 3.1a:

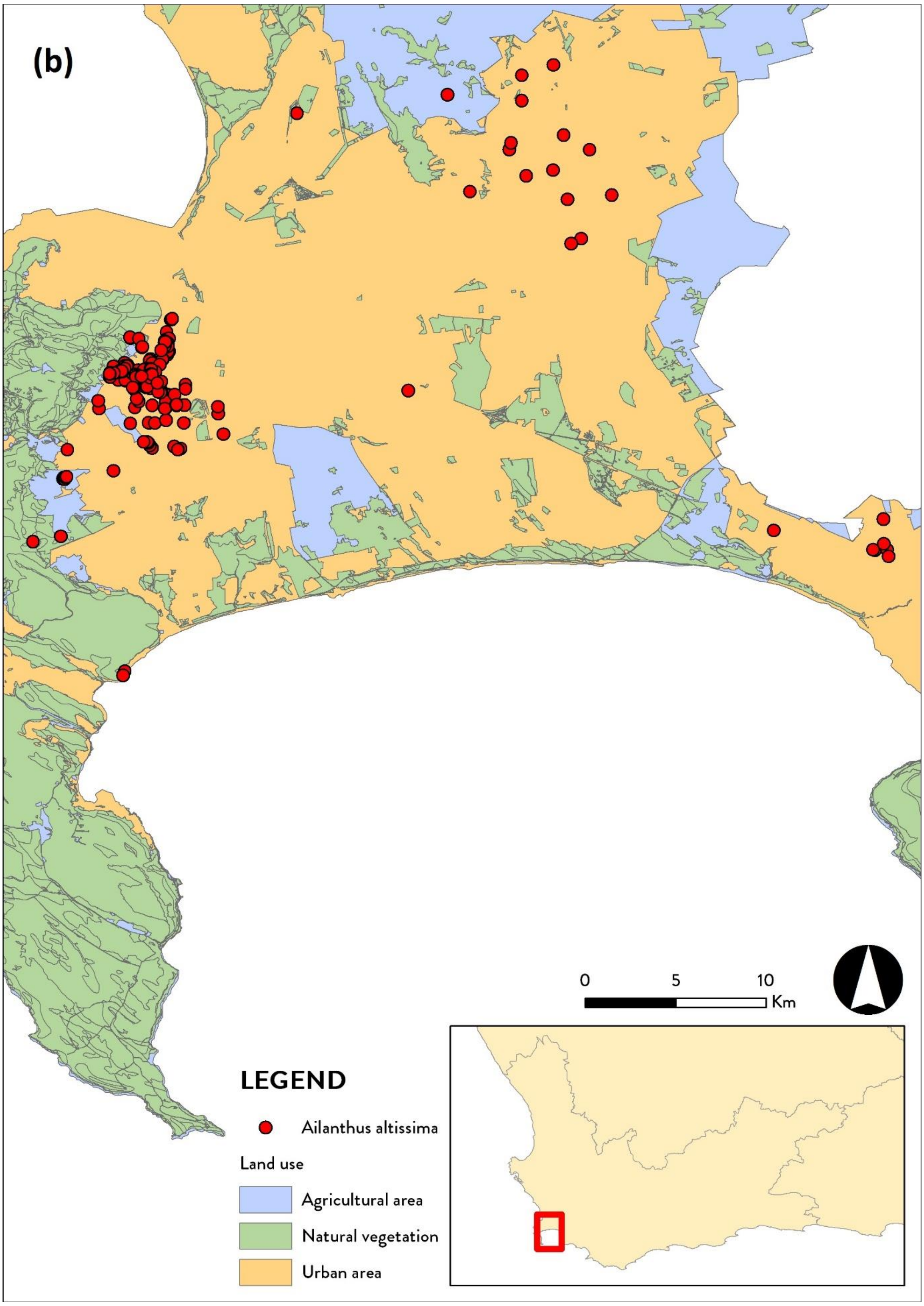
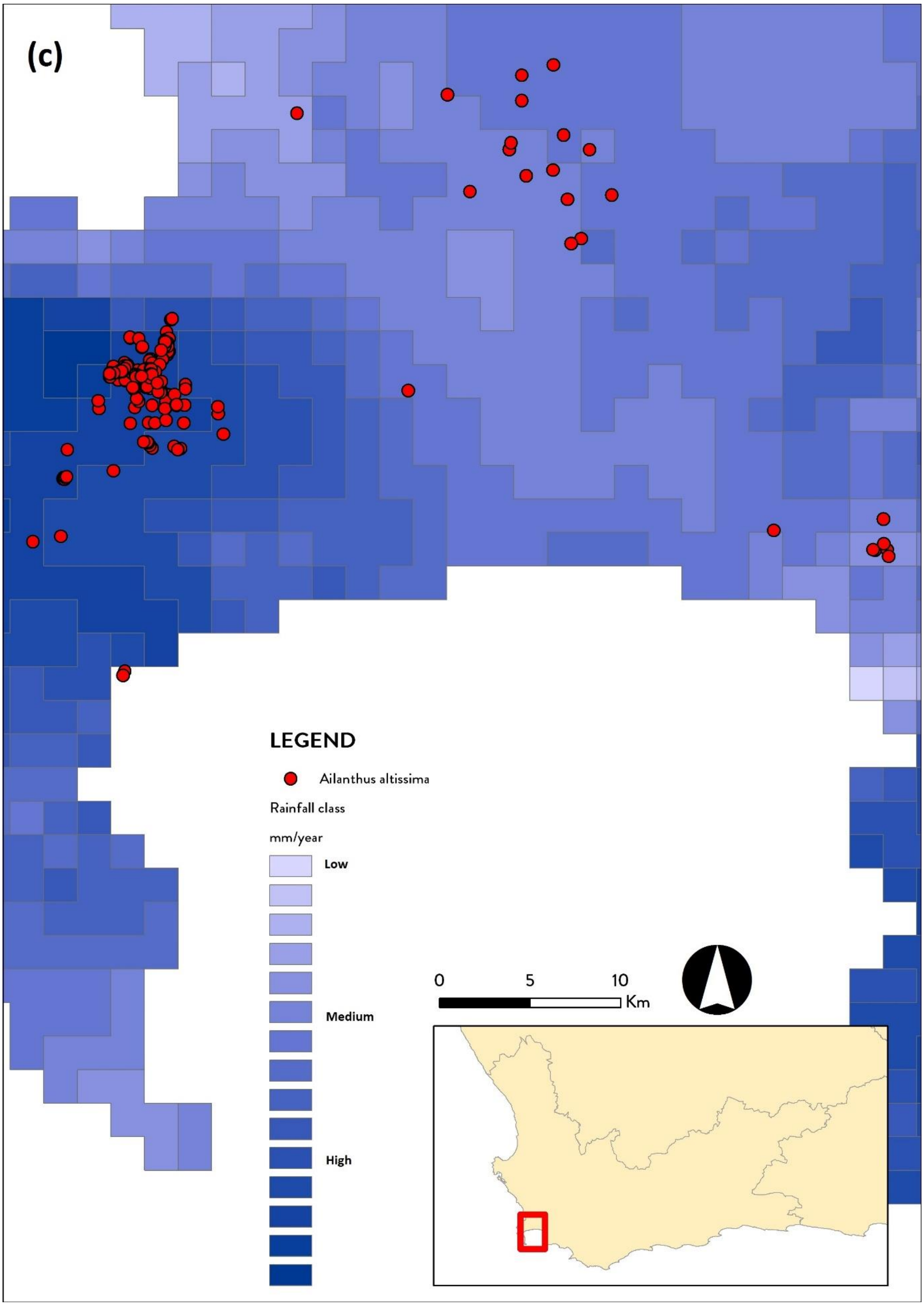

(b)
0
5
10
Km
LEGEND
Ailanthus altissima
Land use
Agricultural area
Natural vegetation
Urban area

Figure 3.1b:



(c)
LEGEND
Ailanthus altissima
Rainfall class
mm/year
Low
Medium
High
0
5
10
Km

Figure 3.1c:

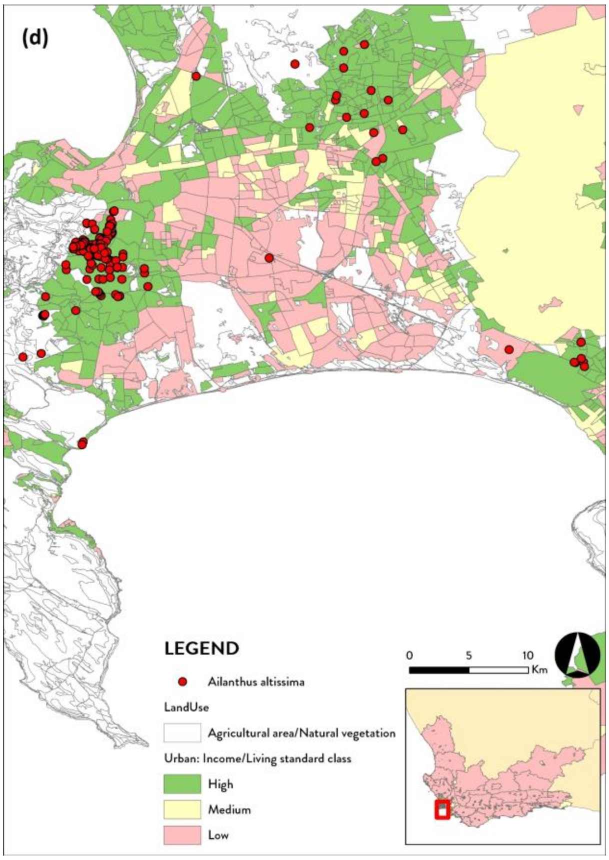


Figure 3.1d: Spatial analysis of *Ailanthus altissima* distribution in Cape Town as per (**a**) soil type, (**b**) land use type, (**c**) rainfall class, and (**d**) per income class in the city. The following soil classes are indicated in the figure: AB = Red and yellow in colour, massive or weak structured soils with low to medium base status occurring at a depth of ≥ 750 mm; CA = Soils with a marked clay accumulation, strongly structured and a non-reddish colour. Occurring at depths of between 450 mm and 750 mm; EA = Soils with minimal development, usually shallow on hard or weathering rock, with or without intermittent diverse soils. Lime rare or absent in the landscape. Occurring at depths of between 450 mm and 750 mm; ED = Greyish, sandy excessively drained soils occurring at a depth of ≥ 750 mm; FA = Soils with a sandy texture, leached and with subsurface accumulation of organic matter, iron and aluminium oxides, either deep or on hard or weathering rock. Occurring at depths of between 450 mm and 750 mm; GA = Rock with limited soils occurring at a depth of ≥ 750 mm. Rainfall was classified as low (< 475 mm/yr); medium (475 – 758 mm/yr); high (≥ 758 mm/yr).

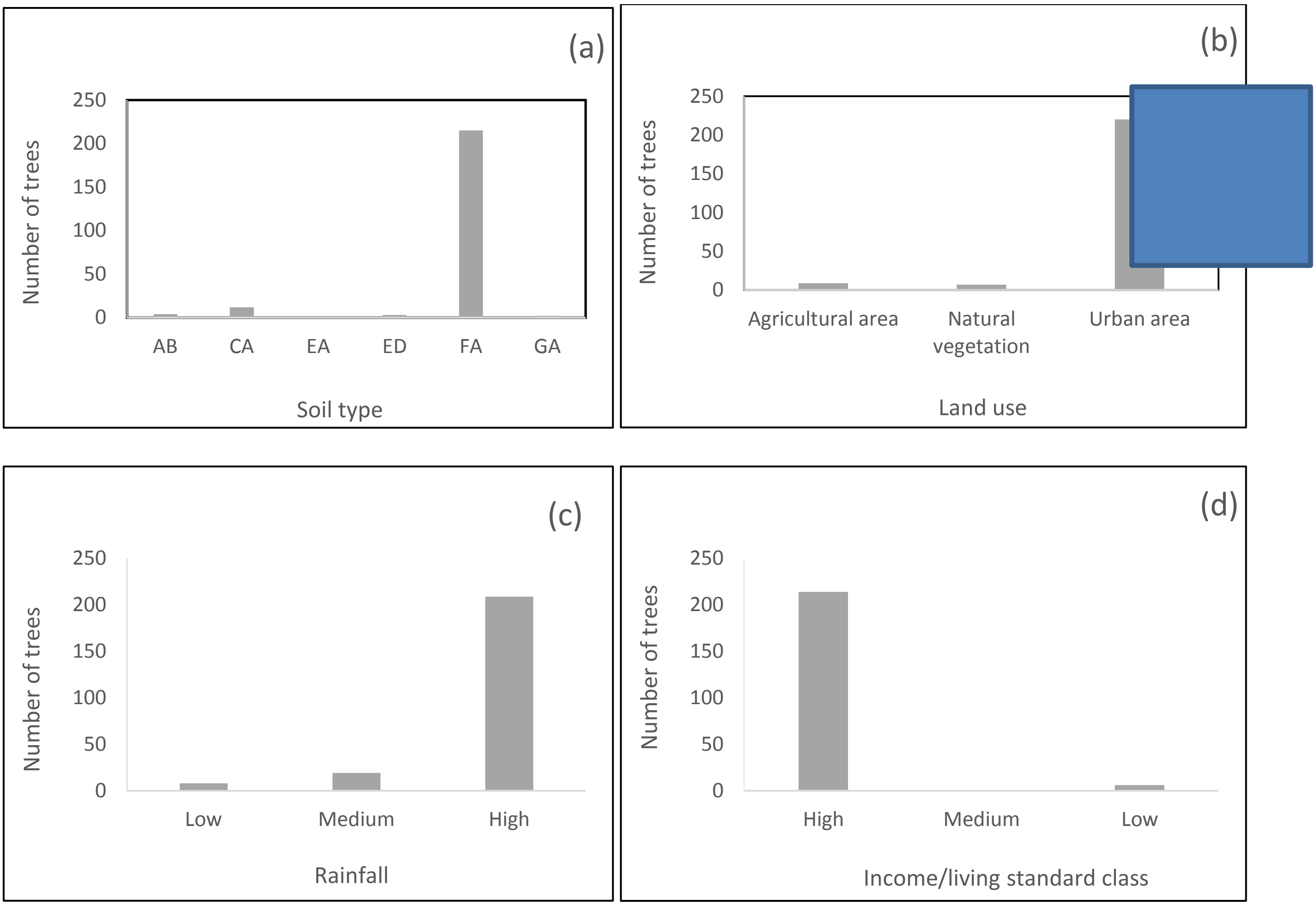


Figure 3.2: Number of individual *Ailanthus altissima* trees per (**a**) soil type, (**b**) land use type, (**c**) rainfall class, and (**d**) per income class in the city of Cape Town.

Clear trends were exhibited in terms of the current distribution of *A. altissima* within the City of Cape Town. We found that *A. altissima* occurred mainly on podzolic soils that are predominantly sandy in texture and that are leached with subsurface organic matter, iron and aluminium oxides (n = 215). These soils are encountered at medium depths of between 450 mm and 750 mm. The species was absent from soils in which minimal levels of development were exhibited. *Ailanthus altissima* occurred mainly in urban areas (n = 220) with a high average household income (n = 214). The species was rare in agricultural (n = 9) and natural areas (n = 7). Furthermore, it was established that *A. altissima* occurred mainly in areas with high average annual (> 758 mm/yr) (n = 209). The species was rare in areas with low rainfall (< 475 mm/yr) (n = 8).

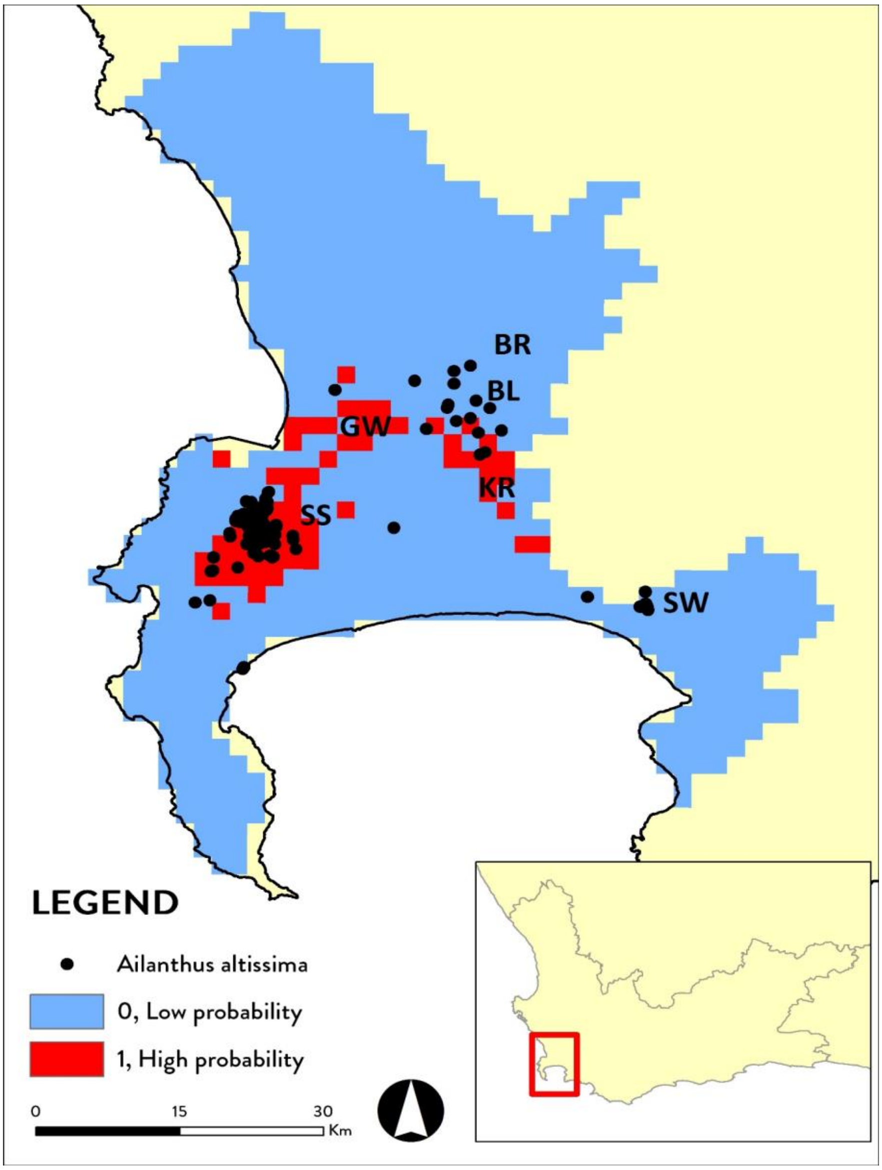


Figure 3.3: Risk map showing potential areas for invasion by *Ailanthus altissima*. Areas with a high probability of being invaded by the species are shown in red; blue shading indicates areas with a low suitability for the species. The following districts are represented in the figure: Southern suburbs (SS), Goodwood (GW), Brackenfell (BR), Bellville (BL), Kuils River (KR), and Somerset West (SW).

Ailanthus altissima is abundant in the southern suburbs and is scattered throughout parts of Bellville, Brackenfell and Somerset West. There is much potential for further spread of *A. altissima* in Cape Town. The southern suburbs and areas around Goodwood and Kuils River are most likely to be invaded by *A. altissima*.

3.4.2 Case study: Newlands

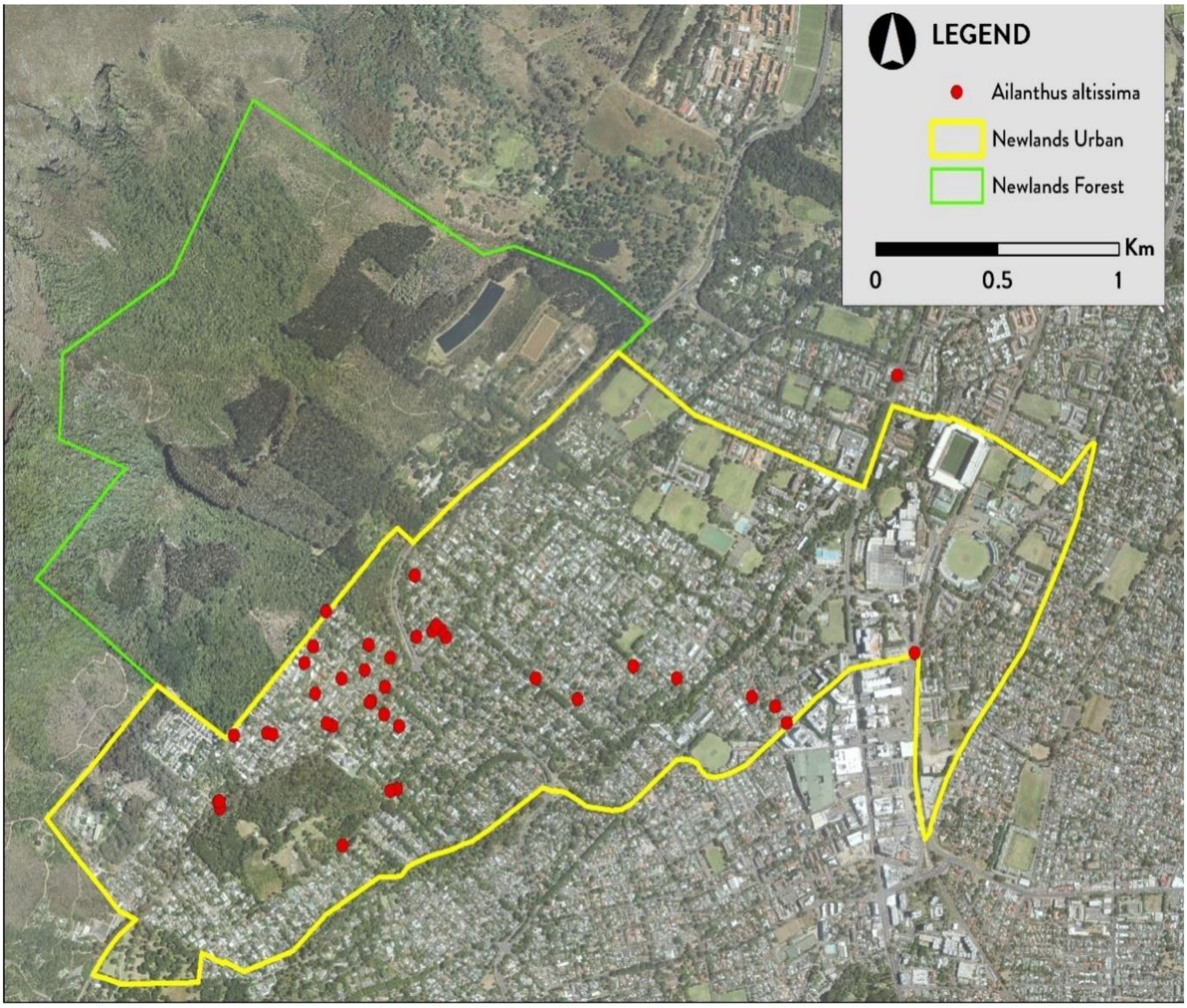
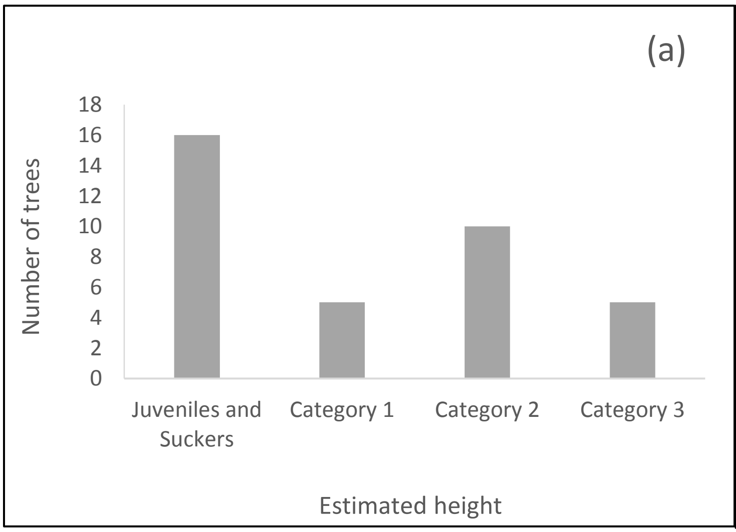


Figure 3.4: The current distribution of *Ailanthus altissima* in Newlands, Cape Town. The urban area of Newlands occurs within the yellow boundary markings; the green polygon indicates Newlands Forest, an area of natural vegetation of high conservation importance within the Table Mountain National Park.



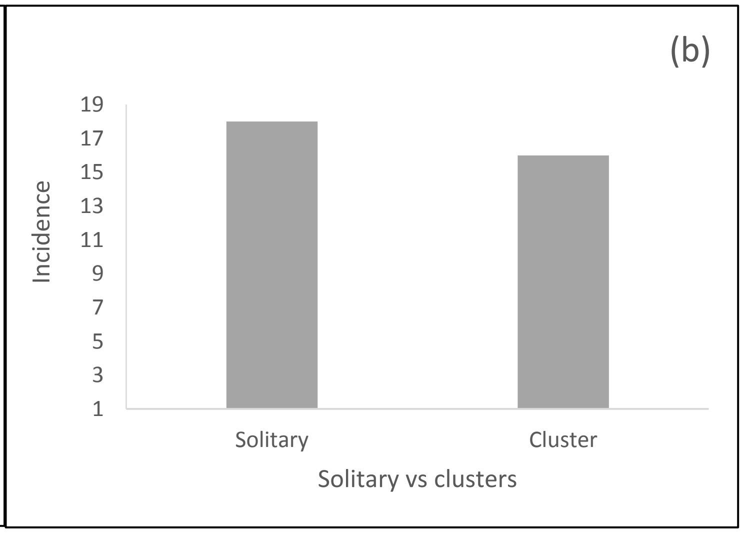


Figure 3.5: Number of *Ailanthus altissima* trees according to age and size class (**a**), and the number of clusters and solitarily occurring *A. altissima* trees occurring in Newlands (**b**). Category 1 refers to all adult tress between one and five metres tall; category 2 refers to all adult trees between five and ten metres tall; and category 3 refers to all adult trees over 10 metres tall.

Table 3.1 Costing scheme for the control and eradication of *Ailanthus altissima* adults and juveniles in Newlands, Cape Town.

Type of cost	Number of adult trees	Number of juvenile	Total cost
Garlon and diesel mixture @ R40.76/plant (adults)	20	*	R 815.20
Garlon and water mixture @ R13.99/plant (juveniles)	*	16	R 223.84
Tree felling services to cut and remove adult trees @ R3500.00 per plant (average)	20	*	R 70000.00
Efekto-Knapsack Sprayer (12 litres) @ R435.00	20	16	R 435.00
Grand total			**R71 474.04**

Newlands falls within a high income, urban area dominated by podzolic soils that are exposed to high levels of rainfall, making it the ideal suburb on which to base this case study. Also, based entirely on database analyses, Newlands appeared to be the suburb with the highest population density of *A. altissima* within the city.

A total of 20 adult *A. altissima* trees and 16 juveniles (occurring in clusters) were found in Newlands. Of the 20 adults, five were between 1 and 5 m tall (category 1), ten were between 5 and 10 m tall (category 2), and five were > 10 m tall (category 3). All juveniles and suckers were grouped in clusters. A total of 16 clusters were counted. Using these data, together with the prices of herbicides, herbicide applicators, diesel, and tree felling services, I calculated the overall cost to control and eradicate all *A. altissim*a plants in Newlands as ca. R71 474.04 (Table 3.1). I determined that the average cost to control a single mature *A. altissima* tree is ca. R3540.76 (this includes the price to cut down and remove mature trees by the tree felling company as well as the associated herbicide, herbicide applicator and diesel prices). Eradication of all adult *A. altissima* trees in Newlands would cost ca. R70 815.20. I determined that the average cost to control separate, individual clusters of juveniles/seedlings/suckers is ca. R13.99 per cluster. Eradication of all clusters in Newlands would cost ca. R223.84.

3.5 Discussion

3.5.1 Spatial analysis

Using geographic information system (GIS) techniques I identified a clear pattern in the distribution of *A. altissima* in terms of soil type, land-use type, rainfall, and a measure of the affluence of areas (income class). GIS techniques have enabled city managers to map the actual distribution of an invader and to identify areas at risk of invasion in the future by evaluating distribution patterns that are exhibited by certain species (Joshi et al. 2006). In the City of Cape Town *A. altissima* predominantly occupies podzolic soils that are mainly sandy in texture and leached with subsurface organic matter, iron and aluminium oxides. Studies in different parts of its adventive range have shown that *A. altissima* can grow on a variety of natural and human-modified soils, ranging from barren rocky substrates to sandy or clayey loams, and even calcareous, dry and shallow soils (Miller 1990; Singh et al. 1992; Kowarik and Säumel 2007). Best growth is however achieved on nutrient-rich, sandy loam soils (Pan and Bassuk 1985; Miller 1990). The results of this study generally confirm those from other parts of the world, except that in Cape Town, *A. altissima* colonizes nutrient-rich sandy-textured soil rather than sandy-loam soils – this was also reported for *A. altissima* growing in Hungary (see Udvardy 1998).

With regard to rainfall preference, *A. altissima* occurred predominantly in areas with high levels of rainfall (≥ 758 mm/yr). Although being largely drought resistant (Trifilò et al. 2004), the species is known to grow in areas that receives annual precipitation of >500 mm/pa (Kowarik and Säumel 2007). *Ailanthus altissima* can tolerate a wide range of climatic conditions, although seasonal variations are known to adversely affect the survival, growth and spread of the species (Kowarik and Säumel 2007). Cape Town has a Mediterranean-type climate with mild, moderately wet winters and dry, warm summers with very little seasonal climatic variation (Cape Town climate, 2015), making the city ideal for *A. altissima* establishment, growth and spread.

Within the City of Cape Town, we determined that the distribution of *A. altissima* corresponds predominantly with wealthier (high-income class) urban areas. Income growth is a primary driver of globalization and clear associations exist between Gross Domestic Product (GDP) and alien species richness in many parts of the world (Hulme 2009). In its native range, *A. altissima* grows as a natural component of broadleaf forests, but in its adventive range the species occurs predominantly in urban environments (Kowarik and Säumel 2007). Within cities, *A. altissima* shows a distribution pattern that is mostly confined to inner city areas with a decreasing frequency occurring along the urban-rural gradient (Kowarik and Säumel 2007). A similar distribution pattern exists in Cape Town; the species is most common in inner city areas with an above-average household income (particularly in the southern suburbs) (Socio-Economic Profile, 2014). The species becomes scarcer along the urban-rural gradient as one moves away from inner-city sections of Cape Town. The abundance of the species in these areas in relation to their associated scarcity in rural areas could be influenced by the historical planting of *A. altissima* (Dullinger et al. 2009). The range expansion of *A. altissima* has been driven by the global dissemination of seeds and the subsequent cultivation of the species for a variety of uses – predominantly as a popular shade and ornamental tree (Kowarik and Säumel 2007). It is highly likely that similar introduction pathways facilitated the establishment and spread of *A. altissima* in Cape Town. Suitable environmental conditions (i.e. podzolic soils and high rainfall) promoted the establishment and spread of the species resulting in the high levels of abundance that are observed in these areas. Unsuitable conditions that occur along the urban-rural gradient as well as the historical planting of the tree could explain the decrease in abundance that is observed in areas existing outside of the inner city.

Areas with a high invasion potential (Fig. 3.3) occur predominantly in the inner-city areas of Cape Town, in particular throughout the southern suburbs and around Goodwood and Kuils River. There is large capacity for spread when we compare the current distribution of the species to all areas identified as having a high invasion potential. Areas identified as having a high invasion potential are all high-income urban areas with podzolic soils that receive high rainfall. This is in accordance with environmental and demographic conditions that are known to promote the establishment and spread of *A. altissima* throughout its adventive range globally (Kowarik and Säumel 2007). The combination of environmental (soil and rainfall) and demographic (land use and income class) features have been commonly used to generate risk maps that highlight potential invasion hotspots (see Hulme 2009 and Jiménez-Valverde et al. 2011), and the use of these in this study gave us an accurate representation of where the species may spread to in the future.

The large area that I determined to be suitable for future invasion versus the current distribution of the species indicate that *A. altissima* is still at an early stage of invasion in Cape Town, and not at equilibrium with environmental conditions. The species is expected to expand its range – in the absence of management – when established individuals reach maturity and act as new seed sources (Potgieter et al. 2014). The species is abundant and widespread in some parts of the city but the potential for spread far outweighs the current distribution. Management interventions are needed to prevent the spread of the species into areas that are currently unoccupied while controlling and containing the spread of the species in areas where it is already present. The southern suburbs should be prioritized for management.

3.5.2 Case study: Newlands

Ailanthus altissima is classified as a category 1b invader in the regulations of the National Environmental Management: Biodiversity Act (NEMBA). Land owners that have category 1b invasive species growing on their land are required to develop and submit a control plan for preventing further spread of the species (Wilson et al. 2013; Gaertner et al. 2016). The suburb of Newlands and the Newlands Forest (which forms part of Table Mountain National Park) are narrowly separated by the multi-lane M3 motorway that serves as a major entry and exit point to the southern suburbs of Cape Town. Natural and semi-natural areas that occur at the urban/wildland interface are vulnerable to invasion by introduced plants with suburban gardens acting as significant sources of alien propagules (Alston and Richardson 2006). The proximal relationship between the two areas increases the potential for *A. altissima* spread from the urban area into the natural environment and, as such, Newlands should be identified as a priority area for *A. altissima* management in Cape Town. Similar cases were observed in pines (*Pinus* species) which were grown in plantations, and Australian wattles (*Acacia* species) which were planted for dune stabilization along the coast (Gaertner et al. 2016). Species from both these genera have since spread into natural areas – a trend that could be repeated by *A. altissima*.

I sampled every road in Newlands which allowed us to accurately quantify the population structure of the species. Our approach, though effective, is limited in that it can only quantify species presences or absences that were visible along the roads that were travelled. The potential presences of species occurring in private properties cannot be accurately quantified due to inaccessibility to private land as well as the unrealistic and uneconomic possibility of entering and sampling every property in Cape Town. As such, the true size of the population may be somewhat underestimated. Remote sensing techniques have been identified as a potential solution to this problem (Joshi et al. 2004). However, there are more advantages associated with our approach in relation to using remote sensing techniques that utilize hyperspectral imagery. One such advantage is that we could locate smaller individuals (that would not appear in hyperspectral images) and assess the age structure of the plants that were encountered. This ultimately gave us a more accurate representation of *A. altissima's* population structure in an area.

Our approach identified a total of 36 *A. altissima* trees in Newlands (16 juveniles and suckers and 20 mature adults). This relatively low population size makes local eradication a viable option in Newlands (Wilson et al. 2013). Management of *A. altissima* is best achieved through an integrated vegetation management (IVM) scheme that targets sexually mature individuals (i.e. adult male and female plants) using a mixture of control techniques (Gover et al. 2004). Foliar applications have been identified as the best method for controlling *A. altissima* juveniles, and cut-stump and herbicide applications are considered to be the best methods for controlling *A. altissima* adults (DiTomaso and Kyser 2007). Herbicides containing imazaypr and triclopyr are most effective at preventing re-sprouting and regeneration of the species (DiTomaso and Kyser 2007). *Ailanthus altissima* is capable of resprouting from both root and stem fragments (Burch and Zedaker 2003; Kowarik and Säumel 2007) which means that follow-up treatments are crucial to prevent re-sprouting. Unfortunately, the costs associated with treating mature plants are higher than the costs associated with the treatment of juveniles, as seen in this study. In terms of long-term planning however, the eradication of mature plants will prevent future population growth and spread of the species by eliminating the sexually reproductive capacity of mature plants (DiTomaso and Kyser 2007). In accordance with the findings of these studies, we suggest that an IVM approach be applied to *A. altissima* in Newlands with mature plants being prioritized ahead of juvenile plants for eradication. Considering all these aspects, we estimate that the overall cost of eradicating *A. altissima* in Newlands would be ca. R71 474.

Although containment and impact reduction are viewed as the most appropriate tactics for managing emerging invaders (van Wilgen et al. 2011), this case study shows that local eradication of an urban invader is achievable when focus is given to a single district. Newlands forms part of the broader southern suburb area that we identified as an *A. altissima* hotspot. A systematic approach that eradicates the species on a per suburb basis would over time, ensure large levels of success. In agreement with van Wilgen et al. (2011), management of invasive species would best be achieved by 1) reducing the measurable impacts associated with an invasive species to acceptable levels in invaded areas, and 2) to prevent spread of the species into unoccupied areas. We suggest that systematic sampling of individual suburbs should be implemented prior to the implementation of an IVM to accurately gauge the population structure and extent of an emerging invader. This will ultimately ensure that the full extent of the problem is understood before attempting to manage it.

3.6 Conclusions

Fine-scale elucidation of invasive species distributions is best achieved using geographic information system (GIS) techniques. The use of GIS techniques has improved invasive species control efforts by enabling managers to identify and evaluate potential trends in the distribution patterns that are exhibited by certain species. These findings help to identify likely areas for future invasion and help delimit areas that are unsuitable for the establishment of an invader, ultimately saving both time and money. The use of GIS techniques was helpful in this study as it allowed me to identify distribution patterns exhibited by *A. altissima* in the City of Cape Town and to identify areas at risk of invasion by the species in the future. I determined that *A. altissima* has a preference for affluent urban areas with podzolic soils that are exposed to high levels of annual precipitation. Identifying these trends enabled me to develop an accurate risk map for the entire City of Cape Town which shows that in relation to the current distribution of *A. altissima*, there is a large capacity for future spread within the city. This approach can be used on all invasive species in urban areas. The systematic sampling approach that we used to gauge the population structure of *A. altissima* in Newlands is an effective method that should be repeated on other emerging invaders in urban ecosystems as it enables an individual to understand the full extent of a species' invasion status. We suggest that the systematic extirpation of emerging invasive species such as *A. altissima* on a per suburb/district basis is a sound approach for preventing the wide-scale spread of such species. It is, however, important to accurately evaluate the population structure of such species before initiating eradication efforts at a fine scale. Ultimately, control efforts used to extirpate certain emerging invaders will differ from species to species however this study shows that an Integrated Vegetation Management (IVM) approach using a mixture of control techniques would achieve the best results when it comes to the control of *A. altissima* in the City of Cape Town.

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CHAPTER 4: THESIS CONCLUSIONS

This project had various aims and objectives, its ultimate aims being to establish the potential range of *A. altissima* in South Africa and to evaluate potential options for management in urban ecosystems. A multi-scale analysis (global, country and regional scales) was used to determine the current and potential distribution of the species. This approach shed new light on the invasion ecology of *A. altissima* and identified key climatic, land use and human mediated disturbance factors that promote the spread of the species. Although the species is not a recent introduction in South Africa, there is still a large capacity for further spread. The approach used in this project accurately identified areas where the species is currently abundant as well as potential invasion hotspots that are susceptible to invasion by *A. altissima* in the future.

The chapters of this thesis contribute new information on many aspects pertaining to emerging invaders in urban ecosystems, and in particular on the dynamics of *A. altissima* invasions in South Africa. Most of the work reported on in the thesis has built on existing literature, but a novel approach was used for mapping the full extent of an emerging urban invader using a multi-scale analysis. Despite the advances made through this work, much remains to be done to improve our knowledge and control of invasive species, especially regarding the management of emerging invasive species and invasive species that occur predominantly in urban ecosystems.

Chapter 1 of the thesis assessed the biogeography, distribution and habitat suitability of *A. altissima* by evaluating the current and potential distribution (based on climatic suitability) of the species at both a global scale and a country scale (South Africa). We determined that the species is confined to the northern and southern temperate zones, and that there is a large capacity for potential spread in parts of South America and Africa. For South Africa, we determined that the species is predominantly confined to urban areas. Species distribution modelling showed that the species has a large capacity for further spread throughout the country. We concluded that the use of various online databases to acquire occurrence data for a particular species is beneficial and largely accurate. These databases do however need to be updated and monitored to ensure that no inaccurate information is added by members of the public. Obviously erroneous records should be removed by the administration in charge of the particular database to ensure that an accurate representation of the distribution of a species is maintained. We can also conclude that climate has a major influence on shaping the distribution of invasive species at a broad scale. Modelling the potential distribution of an invader using climatic variables alone serves as a good first approximation of the potential range of the species. This is, however, not an entirely accurate representation of potential species spread; other environmental factors need to do be incorporated into the design of a model and to accurately determine the full extent of an invader.

Chapter 2 evaluated the degree to which the potential range of *A. altissima* has been occupied in South Africa and identified areas at risk of future invasion. This chapter built on the concepts proposed in Chapter 1 by highlighting the importance of incorporating environmental variables besides climatic factors at various spatial scales to identify areas of high invasion potential. This multi-scale approach facilitates the early detection of invaders and is an important tool for preventing their spread into high risk areas. This approach can be used to accurately identify potential invasion 'hotspots' that are susceptible to invasion by invasive species that occur predominantly in urban ecosystems. This chapter highlighted the influence that human mediated disturbances have on shaping the distribution of *A. altissima*. Future studies should always incorporate the effects of human influence when determining the potential distribution of an invasive species that occurs predominantly in urban ecosystems. Although I am confident that the results of this chapter are accurate, the coarseness of the environmental data that were used could misrepresent the potential spread of *A. altissima* in South Africa. Ideally, it would be beneficial to use environmental data at a finer spatial scale to achieve greater accuracy in predicting the spread dynamics of an invasive species. However, this is often unrealistic, especially when seeking to model the distribution of an invasive species with a large number of occurrence records. More work could be done on the modelling approach to ascertain which methodology could ultimately produce the most accurate output (i.e. most accurate representation of the potential distribution of the species). Also, it could be beneficial to determine whether the species is capable of infiltrating natural ecosystems in South Africa and if so, to determine whether it can spread rapidly and cause impacts in such ecosystems. The species has been known to infiltrate and thrive in natural and semi-natural areas in other parts of the world (see Kowarik and Säumel 2007 and Kasson et al. 2014). It is important to determine whether the same is possible in South Africa and if so, what preventive measures can be taken on a national scale to prevent this from happening?

Chapter 3 evaluated the distribution pattern of *A. altissima* in the City of Cape Town. The overall aim for this chapter was to develop a management protocol for the species by evaluating its distribution at a fine scale. Fine-scale elucidation of invasive species distributions is best achieved using geographic information system (GIS) techniques. The use of GIS techniques helped to identify likely areas for future invasion while delimiting areas that are unsuitable for the establishment of an invader. This approach saves both time and money. The use of GIS techniques was helpful in this chapter as it allowed us to identify distribution patterns and areas that are at risk of invasion by *A. altissima* in Cape Town. Application of this approach showed that the species is capable of spreading into many currently unoccupied areas in the city based on distribution patterns that we identified in terms of the distribution of *A. altissima* according to soil type, land use type, rainfall and income/living standard class. This approach can be used on other invasive species in urban ecosystems and is particularly effective for fine-scale analysis. Occurrence data that we collected was however biased due to oversampling in certain areas (in particular the southern suburbs), and there was under sampling in others (in particular around Bellville and Brackenfell). This could have influenced our results as it is an inaccurate representation of the *A. altissima* population in Cape Town. Another limitation of the study was that some of the environmental data that were available were outdated. Similar studies that aim to utilize the methodology proposed in Chapter 3 should ensure that accurate occurrence data is obtained, and that the environmental data that is utilized has been recently updated.

The systematic sampling approach that we used to gauge the population structure of *A. altissima* in Newlands is an effective method that should be repeated on other emerging invaders in urban ecosystems. The approach helps to understand the population structure of an invasive species, which is important for the development of a management protocol. Inaccessibility to some private property and the unfeasibility of sampling every property within a suburb can result in the underestimation of the true population size and structure of a particular species. To rectify this problem, the approach presented in this chapter could be combined with remote sensing techniques to improve the estimation of the full extent of invasive species in urban ecosystems. Although this combined approach may improve invasive species inventories in urban ecosystems, it too will not be able to precisely evaluate the full extent of an invader (i.e. there will still be a few individuals that remain undetected).

The multi-scale analysis presented in this project is an effective method for accurately evaluating the distribution of an emerging, urban invader. The analyses presented in this paper are accurate and I believe that I have managed to evaluate the current distribution, establish the potential distribution and identify environmental drivers that have an effect on the distribution of *A. altissima* in South Africa; and in Cape Town in particular.

There are still large gaps in our knowledge of *A. altissima* and invasive species management in general in South Africa and internationally, and better understanding of these gaps could improve the management of *A. altissima*. Some key issues that require further research are listed below.

- The costs of mechanical and chemical control of *A. altissima* in South Africa are high, and cheaper alternatives for controlling the spread are needed.
- A potential biological control agent (*Verticillium nonalfalfae*) has killed large numbers of *A. altissima* trees in parts of North America (see Kasson et al. 2014). Tests need to be done in other parts of the world to ascertain the potential of *V. nonalfalfae* as a potential biological agent for the control of *A. altissima* under different conditions.
- Research and testing of further biological control agents is needed.
- More work needs to be done on invasive species in urban ecosystems in South Africa. Few studies have focussed entirely on invasive species in urban ecosystems in this country. With escalations in global trade and long-distance transportation, introductions of exotic species in cities and towns will increase. Studies focussing on the effects associated with urban invasive species as well as their propensity to spread into currently uninvaded areas and factors promoting their spread, are lacking. Cities require a novel approach when it comes to studying invasive species (see Chapters 2 & 3). This approach needs to be formalised to ensure that the current and potential distribution of a particular species can be accurately evaluated and determined. This will enable stakeholders and city managers to develop an accurate management protocol for the control of urban invaders.

APPENDIX 1: ADDITIONAL OUTCOME: CITIES INVADED.

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Why are invasive non-native species abundant in cities?

People collect non-native species for a range of reasons – some are serious plant or animal collectors, while others just like a variety of plants in their gardens. Cities are, by definition, places where large numbers of people live, and they tend to accumulate a variety of new species in large numbers, and this (large numbers of people, a proportion of who collect a large variety of non-native species in a relatively small area) explains why such species are abundant in cities. The growth in the number and size of cities worldwide has also contributed to the problem and South African cities are no exception. Cape Town is an example of a city where invasive species are a large and growing problem. Cape Town has a population of 3.8 million people, and it is growing more rapidly than any other city in southern Africa. Cape Town is also a focal point of the national economy and international tourism, providing avenues and opportunities for the introduction and spread of non-native species within the city and surrounding landscapes. The problems in Cape Town are particularly acute, because the city is located in the Cape Floristic Region, a global biodiversity hotspot. The city's boundaries contain 18 nature reserves, including Table Mountain National Park. Thus, the risk posed to native biodiversity by non-native species that escape is extremely high.

What's the issue? Why bother?

Invasive species can displace native species and, in the worst-case scenario, completely dominate areas. From their strongholds within city environments invasive species can spread into surrounding natural areas, where they can pose significant threats to native species. Almost two-thirds of known invasive alien plants have originated from gardens. Non-native animals kept as pets (e.g. cats and many bird and fish species) can establish feral populations and become invasive if they manage to escape or are deliberately released. Escaped nonnative fish and domestic cats can have significant impacts on wildlife. Several examples from Cape Town illustrate these problems. Pine trees (Pinus species), established to provide timber and to 'improve' the bare mountain slopes, and Australian wattles (Acacia species), planted mainly for dune stabilisation, have spread widely into natural vegetation. Invasive pines and wattles pose serious risks to humans because they increase the severity of wild fires near residential areas (see van Wilgen this issue). Another concern is that criminals use dense wattle stands to hide in. Another non-native species, the tree of heaven (Ailanthus altissima, planted as an ornamental street tree) is highly invasive in the urban environment, and it damages buildings and roads. Floating water weeds (such as water hyacinth, *Eichhornia crassipes* and parrot's feather, *Myriophyllum aquaticum*) were introduced as decorative pond plants, and have spread to block waterways and negatively affect water quality. Some non-native species can also cause serious health problems. Pampas grass (*Cortaderia selloana*, a popular garden plant) and beefwood (*Casuarina equisetifolia*, widely-used as a windbreak and for shade) can both cause allergic reactions, especially to people susceptible to hay fever and asthma. Syringa (*Melia azedarach*), oleander (*Nerium oleander*) and thorn apples (*Datura ferox* and *D. stramonium*) all have potentially lethal parts (berries, leaves or seeds). In addition to plants, non-native animals such as the European paper wasp (*Polistes dominula*) and the German wasp (*Vespula germanica*) can also be problematic. These two aggressive wasp species are a serious nuisance, as well as a potential health hazard for people who are allergic to them. Another urban invader is the house crow, which thrives in an urban environment, living on refuse and becoming a nuisance and health hazard.

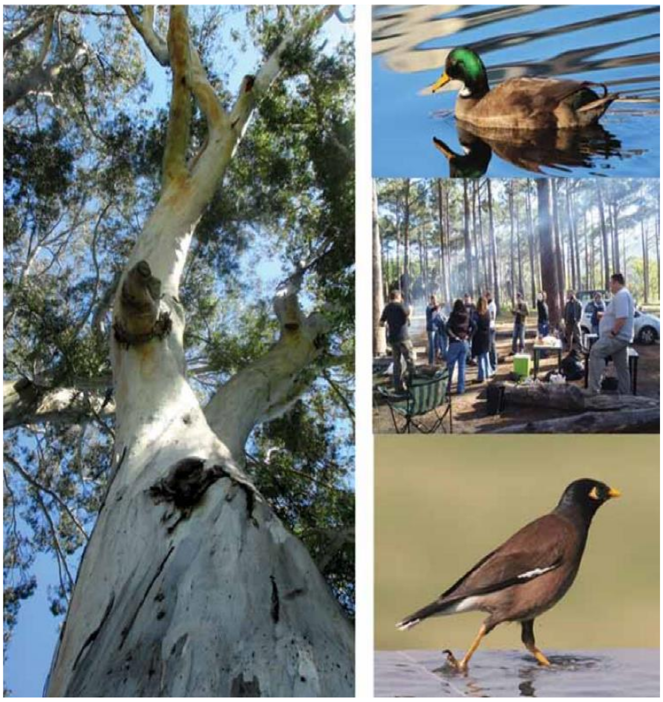

Figure A.1 left: Non-native eucalypt species are seen as ‘culturally native’ in parts of South Africa. Right top: Non-native mallard ducks have established feral populations across Cape Town and are now interbreeding with indigenous ducks. Right middle: Invasive pine trees provide shade and are regarded by some people as more attractive than fynbos shrublands but they are well known for replacing native fynbos species. Right bottom: Common myna (Acridotheres tristis), a highly invasive bird species that is considered a serious threat to native bird species. Image: Sophia Turner, Ulrike Irlich, Lisel McGregor, Dick Daniels (http://carolinabirds.org/).

So let’s get rid of them!

Unfortunately, it is not so easy, as some species pose conflicts. People often have strongly differing views when it comes to non-native species, and these divergent views sometimes lead to conflicts. Trees are particularly controversial, as many citizens regard the trees as attractive and ecologically beneficial, complicating the efforts to control those that are invasive. People can also establish cultural connections with non-native trees. Because they are so long-lived, non-native tress can become associated with a place and be regarded as culturally important by some city inhabitants (e.g. non-native eucalypt species are seen as ‘culturally native’ in parts of South Africa). Examples include Jacaranda trees (Jacaranda mimosa) in Pretoria and English oaks (Quercus robur) in Stellenbosch. Some harmful species are also simultaneously beneficial to certain groups of people or industries. For example, invasive pine trees are well known for replacing native fynbos species but they also provide shade and timber, and are regarded by some people as more attractive than fynbos shrublands. Non-native mallard ducks are another example. They were introduced via the pet trade and have established feral populations across Cape Town and now interbreed with indigenous ducks, contaminating the gene pool of these native species. People are very fond of the ducks and it is common for families to spend time at ponds, feeding these ducks. Of particular concern is the interbreeding with the indigenous yellow-billed duck. In both the cases of alien trees and ducks in the city of Cape Town, control programmes have been seriously complicated by large numbers of people expressing strong opposition to the control.

The way forward: management and policies

All landowners, including municipalities such as the City of Cape Town, are obligated by South African environmental legislation (NEM:BA) to manage certain invasive species that are listed under the Act. This is especially important in Cape Town, given the juxtaposition of protected and urban areas (Box). Cape Town's invasive species control programmes dates back to the 1940s. In 2008 the City established an Invasive Species Management Unit, with an annual budget of R1 million and a dedicated team. Since then, the programme has grown to include areas managed by multiple departments within the city. The City now manages 55 teams, averaging 10 workers each, drawn from impoverished communities. These teams are tasked with the control of invasive plants and animals in terrestrial and aquatic ecosystems. They are also responsible for the early detection of emerging invasive species and implementing control measures as quickly as possible to control and if possible eradicate them. Although originally funded by the City's ratepayers, additional and substantial funding has been obtained from the Working for Water programme and other sources, increasing the available funds to more than R20 million in 2014. Nature reserves are given first priority, followed by areas where invasive plants are a fire hazard or provide shelter for criminals and areas in which there are small populations of an invasive species which can be easily controlled. Another approach being piloted by the City is the promotion of indigenous plant species over non-native ones. This approach is undertaken in tandem with alien species control operations so that people have viable alternatives for providing variety in their gardens, shade or screening. This positive aspect of the city's operations also helps to reduce any negative perceptions associated with control operations.

How can you get involved?

The City of Cape Town has several organisations that provide opportunities for you to get involved. You can join your local 'Friends' or NGO groups, generally associated with nearby nature reserves or conservation areas, to assist with indigenous plant monitoring and emerging weed detection. Alternatively, you can join your local hack group to assist with invasive plant clearing. You can also log records of invasive species on iSpot (www.ispotnature.org) or become a member of Cape Town's Spotter Network on www.capetowninvasives.org.za. You can join the Facebook page Cape Town Invasive Species for more information about invasive species in and around Cape Town. You can also take active measures like not planting invasive species in your garden, or being more careful about how you dump garden waste, so as not to spread unwanted species. Other cities in South Africa have similar initiatives (see for example http://www.durbaninvasives.org.za/).

NEM:BA alien and invasive species regulations

In October 2014 the Alien and Invasive Species regulations of the National Environmental Management: Biodiversity Act (NEM:BA) became law. These regulations are aimed at preventing the introduction and further spread of invasive and potentially invasive species. In practice the regulations consist of a list of invasive organisms (plants, animals and microbes) and a list of species prohibited from being imported into the country. The list of invasive organisms groups species into four different categories, with specific management and control requirements for each category (Table 1). All landowners (private, business and government) in South Africa are required to comply with these requirements under the Act. The City of Cape Town, as a major landowner within the municipal boundaries of Cape Town, is no exception to this and is already in the process of implementing the NEM:BA regulations. As a first step the City needs to know what listed species are on municipal land. To this end the City is using its spotter network (on www.capetowninvasives.org.za) to record data on listed non-native species. This distribution information is then being used to support control operations aimed at (1) eradicating all category 1a species, and (2) developing a management plan for future invasive species control. The presence and density of invasive species that occur on all City-owned land is being mapped and appropriate control measures put in place to reduce the impact of such invasive species. The City of Cape Town is leading the way in this regard and it is hoped that these experiences can be used to develop guidelines for other municipalities to become compliant with the new regulations.

For more information on the NEM:BA AIS regulations visit: http://www.invasives.org.za/legislation.html

Table 1: Categories used to define legal requirements for listed invasive organisms in South Africa

Categories	Legal requirements
Category 1a	Invasive species that must be eradicated if possible (or controlled if not). Trade, planting or propagation is prohibited.
Category 1b	Invasive species that must be controlled and, where possible, eradicated. Trade, planting or propagation is prohibited.
Category 2	Invasive and potentially invasive species for which a permit is required to carry out a restricted activity. This category includes commercially important species such as pines, wattles and gum trees.
Category 3	Invasive species that need not be controlled or removed (sometimes just for particular areas or provinces). However, no further planting, propagation or trade is permitted.

Box 4.1 NEMBA alien and invasive species regulations

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