Niche requirements and breeding system of *Hypericum pseudohenryi*, an invasive plant species in South Africa

By

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PREFACE

All the work described in this thesis was carried out at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa, from January 2014 to May 2016, under the Supervision of Dr. Andreas Jürgens and Co-supervision of Prof. Steven Johnson.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, represent original work by the author and has not been submitted in any form to another university. Where use has been made of the work of others, it has been duly acknowledged in the text.

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Carryn Leigh Smith

May 2016

I certify that the above statement is correct and as the candidate's supervisor, I have approved this thesis for submission.

Andreas Jürgens

………………………………… ……………………………………….

Honorary Associate Professor Andreas Jürgens Professor Steven Johnson

Supervisor Co-supervisor

DECLARATION: PLAGIARISM

I, Carryn Leigh Smith, declare that

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Carryn Leigh Smith

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ABSTRACT

Invasive alien species threaten ecosystems throughout South Africa through alteration of the habitat and loss of biodiversity. Emerging invasive alien plants are those that have small populations, but have the potential to spread and cause widespread damage in the future. One of these emerging invasive alien plants, *Hypericum pseudohenryi*, came from China as an ornamental plant, and has invaded the KwaZulu-Natal Drakensberg and Midlands and mountains of the Eastern Cape. There is little published information about *H. pseudohenryi*, both in the native range and the invaded range. To help create better management plans for *H. pseudohenryi* in the future, experiments were done to determine whether the species is self-compatible and to determine the potential spread of the species across South Africa. Breeding system experiments found that *H. pseudohenryi* is self-compatible and is able to produce small numbers of seeds via autogamous self-fertilisation. This indicates that there is a high risk of new populations being formed from a single founder individual. Climate niche modelling using current climatic conditions revealed that *H. pseudohenryi* has not yet realised its full climatic niche in South Africa. As the climate changes in the future, climate niche modelling showed that the range of climatically suitable habitat of *H. pseudohenryi* is contracting into high altitude areas of the Drakensberg. These findings suggest that *H. pseudohenryi* requires intense management, especially in the Drakensberg area, to contain the spread of this emerging invasive species.

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I can do all things through Christ, who strengthens me – Philippians 4:13

Table of Contents

List of Tables

Table **Page**

List of Figures

Figure **Page**

Chapter 1

Introduction

1.1. Rationale for research

Invasive alien plants (IAPs) have become a feature in many landscapes across the world, causing damage to ecosystems (van Wilgen *et al.*, 2008). Although many plant species have been moved around the world for various reasons, such as forestry, ornamental trade or accidently through fodder contamination, only 20% of these plants become invasive and require management plans to prevent further damage to the ecosystem (Pimentel *et al.*, 2001). Many IAPs threaten ecosystems because of habitat alteration. Changes in vegetation structure affect microclimate, nutrient cycling and hydrological processes (Coetzee *et al.*, 2007, Bird *et al.*, 2013, Le Maitre *et al.*, 2014). Often, the result of these alterations leads to a positive feedback mechanism, where the IAP flourishes to the detriment of the local flora and the fauna that rely on native plants (Richardson & van Wilgen, 2004, Samways & Taylor, 2004).

Introduced plants still considered being in the lag or early colonisation phases of invasion are known as emerging weeds. These plants have populations' small enough to be completely eradicated through proper management of the species throughout its range in South Africa. One of these emerging weeds, invading the KwaZulu-Natal Drakensberg, Midlands and Eastern Cape, is *Hypericum pseudohenryi* (Carbutt, 2012). Native to western China, it is thought that *H. pseudohenryi* was brought to South Africa as an ornamental plant. Very little information about *H. pseudohenryi* is known, both in the native range and in the invaded range in South Africa. At present, South Africa is the only country to have reported *H. pseudohenryi* as invasive. More information about the biology of *H. pseudohenryi* and its potential to spread is required in order to make informed management decisions to eliminate it from South African ecosystems.

1.2. Aims and Objectives

This thesis aims to address three main objectives: 1) to review the impact of invasive alien plants in South Africa, their effect on South African ecosystems and management options for these species, 2) to determine whether *H. pseudohenryi* is self-compatible in its South African range and

3) to determine the potential extent of spread of *H. pseudohenryi*, both under current climatic conditions and under future conditions with climate change.

Chapter 2 examines invasive alien plants in South Africa. Characteristics common to invasive alien plants in South Africa and the effect that IAPs have on South Africa ecosystems is analysed. The management of IAPs in South Africa is critically analysed, especially with regards to recent legislation changes around IAPs. From the concepts presented in the review, specific aspects of plant invasions in South Africa will be looked at in detail using *Hypericum pseudohenryi*, an emerging invasive in South Africa. These aspects include reproductive strategies and possible spread into climatically suitable habitats. Management of *H. pseudohenryi* will be discussed in the final chapter using the framework from Chapter 2 to give recommendations for the species.

In Chapter 3, the prevalence of self-compatibility of *H. pseudohenryi* in three South African populations is assessed. Breeding system experiments were done *in situ* in three established populations, at Monk’s Cowl and Giant’s Castle in the KwaZulu-Natal Drakensberg and at Mbona Private Game Reserve in the KwaZulu-Natal Midlands. Seeds collected from the breeding system experiment were tested for germination success in the lab on an artificial growth medium, to determine if inbreeding depression exists in South African populations of *H. pseudohenryi*.

Chapter 4 assesses the extent to which *H. pseudohenryi* could spread across South Africa using climate niche modelling. Under current climatic conditions, the climatic niche of *H. pseudohenryi* in South Africa is considered using population data from China as well as South Africa, to determine of there has been a climate niche shift in the invasive population. Using predicted future climatic conditions, habitat that is climatically suitable is assessed for two different climate change scenarios.

Finally, in Chapter 5, results and conclusions are synthesised and summarised for Chapters 2 to 4. The impact of *H. pseudohenryi* and its management in South Africa is addressed, with recommendations for categorisation on the list of declared weeds in the National Environmental Management: Biodiversity Act as outlined in Chapter 2.

Chapter 2

Causes of alien plant invasion and its consequences on South African ecosystems: A review

ABSTRACT

South Africa has at least 600 invasive alien plant (IAP) species found in all biomes around the country, which threatens biodiversity across the landscape. One of the main challenges in the management of IAPs is discovering plants that have the potential to become invasive in the country. Despite numerous attempts at identifying a general set of traits that are characteristic of IAPs, not all plants that become invasive have these traits. Identifying a set of traits would help to screen plants before they enter a country to prevent plants naturalising in the new environment. In some cases, particular habitats are vulnerable to invasion due to certain characteristics of the habitat. Invasive alien plants are a particular problem in South Africa, as the country has a high rate of endemism, especially in the Fynbos biome. The main threat of IAPs on biodiversity is habitat alteration, causing changes to vegetation structure, nutrient cycling and hydrology. As South Africa is a water-scarce country, the effects of IAPs on water are of major concern. This review attempts improve the understanding of IAPs in South Africa through understanding specific traits of plants that make them invasive, and what habitats are susceptible to invasion. The current knowledge of the characteristics of IAPs in South Africa is summarised. Characteristics of habitats in South Africa that are vulnerable to invasion are also discussed. Finally, an overview of management of IAPs in South Africa will be examined.

2.1. Introduction

Since the beginning of human global travel approximately 500 years ago, alien plants have become a feature of many landscapes globally (Mack *et al.,* 2000, Hierro *et al.,* 2005). While some plants have remained non-invasive in the new environment, or their populations died out due to various factors (Mack *et al.,* 2000), up to 20% of introduced species have become problem plants, resulting in damage to local biodiversity and substantial costs to the economy (Pimentel *et al.*, 2001). Some invasive alien plants (IAPs) were introduced accidently through contamination with fodder or crop seeds (e.g. *Parthenium hysterophorus* L.). Many IAPs, however, were introduced for use in forestry (e.g. *Acacia mearnsii* De Wildeman) or the nursery industry (e.g. *Lantana camara* L.) (Whitney & Gabler, 2008, Richardson & Rejmánek, 2011). Once introduced, whether by accident or for industry, the effects of IAPs can have severe negative consequences for the environment.

There are 600 alien plant species listed in South Africa on the South African Plant Invaders Atlas (SAPIA) database (2007) and of these, 50 species accounted for the majority of invasions around the country (Henderson, 2007). Most research on IAPs in South Africa has focussed on invasive alien trees (e.g. Le Maitre *et al.*, 2002, van Wilgen & Richardson, 2014), as trees have had some of the worst effects on South African ecosystems. To add to the problem, many of the worst invaders have been resident in South Africa for more than 200 years, allowing time for these species to spread across the country (Henderson, 2006). The species that threaten South African ecosystems the most are within the genera *Acacia, Pinus* and *Hakea,* with areas in the Western Cape, east coast and eastern interior being most affected by invasive alien plants (Richardson & van Wilgen, 2004).

Many ecosystems in South Africa are threatened by IAPs, mainly through loss of biodiversity and habitat transformation (Richardson & van Wilgen, 2004). Invasive alien trees alter fire regimes (Milton, 2004), exclude native vegetation (Le Maitre *et al.*, 2011), but the biggest impact are changes to hydrological processes (Cullis *et al.*, 2007, van Wilgen & Richardson, 2014). As South Africa is a water scarce country (DWAF, 2002), invasive alien trees are a main concern in South Africa due to their large consumption of water resources, which negatively affects river ecosystems in the country (Foxcroft *et al.*, 2007, van Wilgen *et al.*, 2008). A study by Le Maitre *et al.* (2002) found that invasive alien plants reduced streamflow by up to 19 million m^3 per year. Focussed removal of invasive alien plants along rivers through management programmes reduce this impact (Dye & Jarmain, 2004).

Management of invasive alien plants in South Africa is directed mainly through the Working for Water programme, which works to remove invasive alien trees from along riverbanks to improve streamflow (Görgens & Van Wilgen, 2004, MacDonald, 2004). In addition, biological control of invasive alien plants has been successful for several species in South Africa (Zimmermann *et al.*, 2004). These management actions are helped by good legislation on invasive alien plants in South Africa. A list of IAPs has been drawn up and gazetted in the National

Environmental Management: Biodiversity Act (NEM:BA), giving different categories to plants that cause widespread damage and to those of value to the country (South African Government, Gazette No. 37320, 12 February 2014).

This review begins with a consideration of a useful definition of an invasive alien plant. Traits that are common among invasive alien plants in South Africa are discussed and then impacts of invasive alien plants on South African ecosystems are reviewed. Finally, management of invasive alien plants and future perspectives of invasive alien plants in South Africa are examined.

2.2. The terminology applied to invasive alien plants

There are many different definitions of invasive alien plants; some refer specifically to plants' impact on the environment, whereas others refer to the impact on economic activities (Pyšek, 1995). A useful definition needs to reflect both aspects. Importantly, the definition of a plant species as invasive does not necessarily mean that the plant is alien or exotic (Pyšek, 1995). Some indigenous or native plants are becoming invasive. In southern Africa, invasion by native woody species; resulting in bush encroachment, is widespread (Reinhardt, 2012).

Many different terms have been used to describe plants that are not native to a given region (Colautti & MacIssac, 2004). 'Alien', 'exotic', 'introduced', 'non-indigenous' and 'non-native' are synonymous terms which are used to describe a plant that is found in a region due to human mediation that enabled it to overcome major geographical barriers to dispersal (Richardson *et al.*, 2011). An alien plant is termed 'invasive' when individuals in a population outside of the native range are surviving, reproducing and dispersing across the introduced landscape (Blackburn *et al.*, 2011). The word 'naturalised' is a subject of great debate when discussing IAPs; the term is often used synonymously with the above terms (Richardson *et al.,* 2011). However, as well as being moved by humans, naturalisation also means that the plant has overcome the biotic and abiotic barriers to survival and is able to reproduce effectively in the new environment (Richardson *et al.*, 2000, Colautti & MacIssac, 2004, Blackburn *et al.*, 2011).

Plants that are considered weeds are those which grow in areas where it is not wanted and that can have some form of impact on the environment or economy, but are not necessarily alien (Richardson *et al.*, 2011). Weeds tend to describe plants that are problematic from an agricultural point of view. Noxious weeds are used in some countries to describe invasive alien plants, however this term often suggests that a plant has some harmful negative effect on people or places (Colautti & MacIssac, 2004).

For the purpose of this review, an invasive alien plant is defined as plants that are new to the environment, being introduced by humans (Pyšek, 1995), and are able to create widespread, self-sustaining populations that successfully reproduce in natural or semi-natural environments (Richardson *et al.*, 2000, Cronk & Fuller, 2001, Keeley, 2001, Richardson *et al.*, 2011).

2.3. Factors affecting plant invasiveness in South Africa

Attempts to pinpoint a universal set of plant traits that determine invasion potential have not been successful. Invasion occurs in four stages: transport, introduction, naturalisation and spread (Blackburn *et al.*, 2011). The process of invasion is non-linear, following an exponential curve (Fuhlendorf *et al.*, 2012). After being transported out of the native range and plants are first introduced into the new environment, the invasive nature of the species may not be immediately evident because the population is small and controlled (Cronk & Fuller, 2001), and invasion may not occur for decades after the plant is introduced (Brown & Bestelmeyer, 2012). This phase of invasion is known as the lag phase.

The next phase of invasion is naturalisation, which is the rapid increase in population numbers through successful reproduction events (Cousens & Mortimer, 1995, Richardson *et al.*, 2000). Further population gains may be made by propagules that immigrate into the population from other sources (Cousens & Mortimer, 1995). Variables such as drought, flooding, changes in soil nutrients and topography may trigger the increase in population growth by creating a more favourable environment for the species (Fuhlendorf *et al.*, 2012). Once the population is able to replace itself through reproduction over several generations, it can be considered naturalised (Richardson *et al.*, 2011).

Once naturalisation has occurred, the final stage of the invasion process is where the invasive alien plant spreads and becomes incorporated into the floristic landscape of the introduced site (Cousens & Mortimer, 1995, Richardson *et al.*, 2000, Blackburn *et al.*, 2011). Once this final stage of invasion is reached, the plant may be considered a species of concern, which requires management actions to prevent further spread (Cousens & Mortimer, 1995). Unfortunately, it is often only once the species has become naturalised that the relevant conservation authorities become aware of its presence. By this stage, it is already having impacts on the natural landscape of the introduced range (Mack *et al.*, 2000). Although there are many different factors, such as climate, soil type or land use that may cause a plant species to become invasive outside of its native range, it has been difficult to determine which factors can be used to predict invasibility in general

(Blumenthal *et al.*, 2009). Several land use changes are also associated with invasion, such as the introduction of cattle, changes to fire regime and the change in climate associated with global warming (Fuhlendorf *et al.*, 2012). While there is no universal set of characteristics that can be used to determine invasibility, there has been progress made on the invasive traits of specific taxa and habitats that are most vulnerable to invasion (Whitney & Gabler, 2008).

Different biomes in South Africa will have different factors that lead to invasive alien plants naturalising in that specific environment (Hugo *et al.*, 2012). For example, the fynbos is invaded by many plants that have seeds that germinate after fire (Le Maitre *et al.*, 2011, Geerts *et al.*, 2013b). Human mediation also plays a role in the establishment and invasion by alien plants, either as dispersal vectors (van Gils *et al.*, 2006, Kalwij *et al.*, 2008) or by transforming the landscape, making new areas suitable for alien plant populations to invade (Castro-Díez *et al.*, 2011).

2.3.1 Life history factors affecting invasiveness

2.3.1.1 Plant functional traits

Plant functional traits are characteristics that determine the ecological role of a species in the environment they inhabit (Drenovsky *et al.*, 2012). Certain plant traits, such as high growth rate, can be used to characterise plants that may become invasive in a new habitat (Castro-Díez *et al.*, 2011). These adaptations that occurred in the native range may result in a competitive advantage in the introduced range, causing the plant species becoming invasive in the habitat. This can result in IAPs being able to tolerate a wider range of conditions and resource levels compared to non-invasive plant species (Cousens & Mortimer, 1995, Leffler & Ryel, 2012). Invasive mesquite (*Prosopis* sp.) trees have deep rooting systems, narrow sapwood and undergo stomatal closing during the hottest parts of the day, which has allowed their invasion into the Northern Cape, where rainfall is scarce and soils low in nutrients (Dzikiti *et al.*, 2013). Some invasive alien plant species are adapted to better exploit resources in the environment than native species in the community. Species that belong to the Fabaceae family, such as *Acacia* species are able to fix nitrogen through root nodules, and are thus better able to thrive on low quality soils (Le Maitre *et al.*, 2011). Phenotypic plasticity can result in flexible traits that enhances the niche breadth, allowing plants to succeed under novel conditions (Lavergne & Molofsky, 2007). In South Africa, *Echium plantagineum* has successfully invaded a large area due to phenotypic plasticity in plant and seed size (Sharma & Esler, 2008). The study found that plants growing in areas with suboptimal conditions were producing larger seeds, which were better able to provision seedlings when resources are limited, enabling them to survive.

2.3.1.2 Reproduction

Successful reproduction in a novel habitat is one of the most important factors that lead to invasion. Many factors hinder successful reproduction outside of the native range, especially as specialist pollinators associated with the plant may not always move with the plant to its new habitat to facilitate cross-pollination (Burns *et al.*, 2011). In the absence of suitable pollinators or failure to recruit pollinators native to the invaded range, introduced plants need to resort to autonomous self-pollination, which can result in reproductive assurance (Harmon-Threatt *et al.*, 2009, Busch & Delph, 2012). It is from this principle that Baker's rule stems, which states that species capable of uniparental reproduction are more likely to establish populations after long-distance dispersal than those requiring mates (Baker, 1955, 1967). A study of 17 invasive alien plants in South Africa by Rambuda & Johnson (2004) found all study species were self-compatible, and that 12 of these were capable of autonomous self-fertilisation. One of the risks of small populations are the negative effects on individual fitness due to low population density, known as the Allee effect (van Kleunen *et al.*, 2007). It has been noted, however, that Allee effects are minimal in invasive alien plant populations, even in small populations (van Kleunen & Johnson, 2005, Rodger *et al.*, 2013).

Another factor that contributes to invasion success is the time the species takes to reach reproductive maturity (Geerts *et al.*, 2013a). *Acacia elata* is an example of an alien species that has not become invasive despite annual reproductive outputs similar to other invasive *Acacia* species (Donaldson *et al.*, 2014). The study found that *A. elata* began flowering a year later than other invasive *Acacia* species, which could be one of the contributing factors to its low abundance in South Africa, as plants can be eradicated prior to reproductive maturity.

2.3.1.3 Dispersal

Sexual reproduction resulting in seeds increases the success of introduction in invasive alien plants, as this leads to greater dispersal than asexual means of reproduction (Burns *et al.*, 2011). Several factors contribute to seeds ability for dispersal. Small seed size, which is common among many IAP species, means that seeds are more easily distributed to new sites than larger seeds as dispersal can occur through wind or movement by small animal vectors (Rejmánek, 1996, Rejmánek & Richardson, 1996). Long distance dispersal of seeds ensures that new populations of the plant species can be formed at sites far from the original focal point of invasion, while short distance dispersal of seeds helps increase the number of plants in the existing population (Cronk & Fuller, 2001). Successful dispersal of seeds will depend on the availability of vectors for dispersal, and the distribution of habitat types across a mosaic of the landscape (Cousens & Mortimer, 1995). Dispersal of seeds from IAPs are most successful through animal and human vectors, although some IAPs are dispersed by wind or water (Cousens & Mortimer, 1995). Invasive alien plants that have fruit attractive to native frugivores have an advantage, as their seeds can be distributed to different habitats (Jordaan & Downs, 2012). Thabethe *et al.* (2015) demonstrated that two *Turaco* species native to South Africa not only were suitable dispersal agents, but that seeds that had passed through their gut had a higher germination rate than seeds that were just allowed to germinate in the soil. Humans are also a potent vector for IAP seed dispersal. Invasive alien plant species are usually closely associated with the human landscape, which may contribute to the ability for seeds to disperse great distances (Cousens & Mortimer, 1995). A study of dispersal mechanisms of *Chromolaena odorata* by van Gils *et al.* (2006) found that in KwaZulu-Natal, seeds were best dispersed along footpaths and roads.

2.3.1.4 Persistence

An important factor for successful invasion is persistence of the species in the invaded habitat. Persistence is usually as a result of large, long lived seed banks, which enables high recruitment of seedlings in the environment over a long period of time (Le Maitre *et al.*, 2011). One of the reasons *Acacia* species are such successful invaders in South Africa is because they flower almost year round, continually contributing to the seed bank (Castro-Díez *et al.*, 2011). The added propagule pressure saturates seed banks, allowing large stands of seedlings to emerge, usually to the detriment of native species (Le Maitre *et al.*, 2011). Some invasive alien plant species are able to produce thousands of seeds per individual. For example, Spanish broom (*S. junceum*) in the Western Cape has been found to create seed banks of up to 450 seeds per square metre (Geerts *et al.*, 2013a). This problem is exacerbated by seed dormancy, which allows the seeds to remain in the seed bank for long periods of time (Cronk & Fuller, 2001). However, the length of time seeds remain viable in the seed bank has not been established in South Africa (Ruwanza *et al.*, 2013).

2.3.2. Factors affecting invasibility of habitats

2.3.2.1 Abiotic

Abiotic factors, such as climate, disturbance soil nutrient levels and soil moisture content, play a role in determining whether a habitat will become invaded by IAPs. Species composition of a community is constrained by the available resources in that habitat (Leffler & Ryel, 2012). Thus, plant communities are most at risk for invasion when resources are in excess, however, resource fluctuations between months or years can change the invasibility of a community (Davis *et al.*, 2000). For example, in areas of high productivity, where soil moisture content is high and temperatures favourable for growth, levels of invasion are highest, and are exacerbated by IAPs that are able to utilise resources more efficiently than native plants (Richardson *et al.*, 2005). Invasive alien species tend to be found most often in warm temperate and subtropical climates and thus South Africa is particularly vulnerable to invasion (Cronk & Fuller, 2001). Thus it is unsurprising that a survey of invasive species in South Africa found that 121 species originated from the tropics (Henderson, 2006). The study also found that those originating from temperate regions are from Australia and the Mediterranean, which have similar climatic conditions to regions in South Africa. Climatic conditions are one of the main factors determining plant ranges (Rouget *et al.*, 2004). Several studies have been conducted that have found climatic matches between invasive species localities in South Africa and their native distribution (Moodley *et al.*, 2014, Potgieter *et al.*, 2014). However, invasive alien plant species do not always occupy the same climatic niche in the invaded range compared to their native ranges (Beaumont *et al.*, 2009b, Bradley *et al.*, 2010). Shifts in climate niche are not common, but may be due to local adaptations, genetic drift or phenotypic plasticity (Beaumont *et al.*, 2009b). Similarly, climate change may result in areas that were previously climatically unsuitable becoming more suited for non-native species (Bradley & Wilcove, 2009, Bradley *et al.*, 2010). Climate modelling is an important tool for predicting climate change associated shifts of invasive alien plants (Jeschke & Strayer, 2008). However, one of the risks of using climate models to predict a species' future distribution is the assumption that the environmental factors are an accurate indication of a species current distribution (Higgins *et al.*, 1999). Disturbances such as fire, road sides and removal of vegetation cover have large impacts on the invasibility of a habitat (Milton, 2004, Kalwij *et al.*, 2008). In most cases, disturbance creates conditions that are optimal for the establishment of invasive alien plants over native species. For example, if the fire regime of an area is altered, fast growing invasive alien grasses may appear before native grasses, creating a field of unpalatable invasive alien grass (Milton, 2004). Natural disturbances, such as floods, can also create conditions suitable for invasive alien plants to exploit the area (Richardson *et al.*, 2007, Thomas & Moloney, 2013).

2.3.2.2. Biotic

Interactions between invasive alien plant species and native plant and animal species also influence the invasibility of a habitat. These include the number of bare patches where invasive alien plants can establish (Burke & Grime, 1996), other organisms such as pollinators and seed dispersal vectors being available to be utilised by the invasive alien plant (Lloret *et al.*, 2005) and recruitment opportunities (Tilman, 1997). Studies have found that the structure and density of native vegetation influences competitive abilities with invasive alien tree seedlings and is an important factor determining the success of these species (e.g. Rahlao *et al.*, 2014, Morris *et al.*, 2015). Communities that are species rich are often thought to be resistant to invasion, however, there are exceptions (Mack *et al.*, 2000). It is theorised that vacant niches within a community may create vulnerability to invasion (Mack *et al.*, 2000, Hierro *et al.*, 2005), however Richardson *et al.* (2005) found that richness of invasive alien plant species is positively correlated with species richness of indigenous plants**.**

Habitats that have high introduction potential will be at great risk of invasion. The input of new individuals, known as propagule pressure is influenced by many factors, such as number of individuals initially introduced, number of introduction events and species characteristics (Iponga *et al.*, 2009a, Potgieter *et al.*, 2014). Riparian habitats that have rivers running through human settlements allow for multiple opportunities for introduction of invasive alien plant propagules (Richardson *et al.*, 2007). Other vectors, such as animals or prevailing winds that increase seed input into the environment contribute to propagule pressure, increasing the likelihood of invasive alien species in the habitat (Moodley *et al.*, 2014, Mokotjomela *et al.*, 2015).

The enemy release hypothesis states that when a plant species is introduced into an area outside of the native range, it should experience a decrease in population control by natural enemies, such as herbivores or pathogens, which results in a large expansion of the population (Mack *et al.*, 2000, Keane & Crawley, 2002, Blumenthal *et al.*, 2009). The specific plant enemies of that species, such as microbes or herbivores, are usually not present in the introduced range of invasive alien plant species, thus the plants are able to re-allocate resources to traits that will give it a competitive advantage over native plants (Callaway & Ridenour, 2004). One of the suggested reasons for the invasive nature of *Banksia ericifolia* in South Africa is that it is not affected by the fungus *Phytophthora cinnamomi*, which affects other *Banksia* and *Protea* species (Geerts *et al.*, 2013b). *Banksia ericifolia* also has a higher growth rate, which could be because of the release from pathogens (Geerts *et al.*, 2013b). Not all invasive alien species are released from enemies in the invaded range. Despite the Peruvian pepper tree (*Schinus molle*) having invasive traits in South Africa, it has not become an invasive species in part because large grazing herbivores were found to negatively affect seedlings in semi-arid areas (Iponga *et al.*, 2009b).

2.4. The consequences of invasive alien plants for South African ecosystems

As South Africa is well known for having hotspots of endemism, such as in the Fynbos and the Midlands Mistbelt Grassland in KwaZulu-Natal, impacts on natural ecosystems are of great concern. In southern Africa, the top 10 most prominent invaders are found across almost the whole region (Henderson, 2007), thus these species have impacts across a wide range of ecosystems and biomes. ‘Emerging’ invasive alien species also pose a threat to South African ecosystems, with 80% of South Africa vulnerable to invasion by at least one emerging invasive alien species (Mgidi *et al.*, 2007). While natural ecosystems are dynamic systems that change as biotic and abiotic factors fluctuate, when invasive alien plants are introduced, the change exceeds the natural rate at which an ecosystem is able to adapt to changes, leading to extreme alterations in the habitat (Cronk & Fuller, 2001). A ripple effect is created as changes to the soil lead to changes in the plant species composition of the ecosystem (Grant & Paschke, 2012). In turn, change in vegetation structure has an effect on herbivores, which in turn affects predators in the ecosystem (Gerber *et al.*, 2008). All of these alterations to the environment affect the services associated with the ecosystem (Pejchar & Mooney, 2009). Most ecosystem services benefit people and changes in the environment can result in a loss of services, costing the local economy as it makes up for the losses (Pimentel *et al.*, 2001).

2.4.1 South African biomes & ecosystems affected

While all biomes are affected by IAPs, two stand out as being particularly negatively affected: fynbos in the Western Cape and grasslands in the eastern parts of South Africa. Across the whole country, riparian ecosystems are threatened by IAPs (Foxcroft *et al.*, 2007). Alien trees have the greatest impact on South African ecosystems, due to their high water consumption (Dye & Jarmain, 2004) and remain the target of management programmes (van Wilgen & Richardson, 2014). Alterations in the vegetation structure of ecosystems results in loss of vegetation, creating negative impacts on fauna (Coetzee *et al.*, 2007).

2.4.1.1 Fynbos biome

The South African fynbos is a world renowned hotspot of endemism, but is one of the most highly invaded biomes in South Africa, with *Acacia*, *Pinus* and other trees threatening the biome the most (Henderson, 2007). The biggest impacts that IAPs have on the fynbos are changes in vegetation structure and alteration of fire regimes (van Wilgen & Richardson, 2014). Habitat transformation is the process whereby invasive alien plant species are able to alter the fundamental properties of the ecosystem that has been invaded (Dukes & Mooney, 1999, Ehrenfeld, 2003). Changes to ecosystem processes usually begin with changes to nutrient cycles. Introduced species are able to change many nutrient cycles, but most importantly, alter nitrogen cycling within an ecosystem (Mack *et al.*, 2000, Ehrenfeld, 2003). Soils are affected by a variety of changes brought about by invasive alien plants. The invasive alien plant species may alter the soil composition through the introduction of new root exudates and microbial elements, as well as changes to the leaf litter constitution (Grant & Paschke, 2012). Increased litterfall from invasive alien plants increases phosphorus in the soil, as well as increasing the pH of the soil in wetlands in the fynbos (Bird & Day, 2014). Changes in soil nutrients brings changes to community structure as native vegetation is supressed by invasive alien species (Cousens & Mortimer, 1995). Invasive alien plants replace the native vegetation through adaptations resulting superior competition with native plants for resources (Mack *et al.*, 2000) and this is most often seen during the seedling stage. Invasive *Acacia* seedlings in the fynbos outcompete native woody seedlings (Le Maitre *et al.*, 2011) and the seedlings further reduce native vegetation due to the short generation time of IAPs, resulting in populations growing more rapidly than that of native species (Rejmánek & Richardson, 1996). For example, *B. ericifolia* is able to reach reproductive maturity earlier than other indigenous species (Geerts *et al.*, 2013b), which is advantageous, especially in fire prone areas, as *B. ericifolia* will have already produced seeds prior to the fire event. Many fynbos plant species require fire in their reproductive cycles to release seeds to the environment (Geerts *et al.*, 2013b). As a result, invasive alien serotinous species flourish in fire prone areas and their presence results in altered fire frequency. Native species that rely on longer periods between fires for their life cycle are not able to produce seeds before the next fire event (Geerts *et al.*, 2013b). As the fynbos is a hotspot for endemism, management of invasive alien plants is important to protect the native species (van Wilgen, 2012). The fynbos biome is widely studied in South Africa, with many examples of the effects of IAPs on the biome (e.g. van Wilgen & Richardson, 1985, Pretorius *et al.*, 2008, Crous *et al.*, 2012, Bird *et al.*, 2013). Although it is an important biome, studies seem to be biased towards the fynbos, with other biomes being neglected.

2.4.1.2 Grassland Biome

Grasslands are also threatened by *Acacia* species, but also by herbaceous species and invasive alien grasses (Milton, 2004, Henderson, 2007). As grasslands are important for large herbivores, both wild and domestic, changes in the vegetation structure of grasslands negatively affect these animals through loss of palatable grasses (Milton, 2004). Invasive alien grasses often have a higher biomass than native grass species, and thus there are changes in plant litter produced when grasslands are invaded by IAPs. Changes in leaf litter reduce solar radiation, change soil moisture patterns alter temperature balance at the soil surface and change microsites essential for seed germination (Grant & Paschke, 2012). Alteration of microsites results in negative impacts on invertebrate communities. Grasslands invaded by silver wattle (*A. dealbata*) in the Drakensberg region have resulted in altered beetle assemblages, due to changes in shade and temperature (Coetzee *et al.*, 2007).

As biomass increases and low herbivory, moribund plant material in the environment leads to changes in the fire regime of the landscape. Fire intensity and frequency increases with increased fuel loads from IAPs (Dukes & Mooney, 1999, Brooks *et al.*, 2004, Pejchar & Mooney, 2009). Many invasive alien grasses in South Africa are unpalatable to grazers in natural pastures, resulting in large fuel loads, which promotes increased fie frequency (Milton, 2004). Invasive alien species that are abundant throughout the landscape shift the fire regime, which suits the further establishment of their species and reduced environmental suitability for native vegetation (Keeley, 2001). In grasslands, fires will not necessarily become more frequent as a result of invasive alien plants. Decreases in the frequency and intensity of fires will depend on flammability, fuel load and fuel moisture content (Brooks *et al.*, 2004).

2.4.1.3 Riparian ecosystems

South Africa is a water scarce country, with an average precipitation of ±500 mm per year, although rainfall is very erratic between years (DWAF, 2002). Invasive alien plants create great pressure on water resources (Görgens & Van Wilgen, 2004), and in South Africa, which is a water restricted country, invasive alien trees are contributing greatly to the problem (van Wilgen *et al.*, 2008, Reinhardt, 2012). Invasive alien plants, especially trees, reduce surface water, and this could be by as much as 172 x 10^6 m^3 per annum, which is about 4% of registered water use in South Africa (Cullis *et al.*, 2007). Water loss from invasive alien trees is due to high transpiration levels. Transpiration from black wattle is more than double that of native vegetation, especially in dense stands (Dye & Jarmain, 2004). Invasive alien trees are known to have higher water consumption than native species (Le Maitre *et al.*, 2002, Pejchar & Mooney, 2009), leaving the soil dry, which reduces the native vegetation adapted to higher soil water levels. Invasive alien species can be more tolerant of drought conditions, resulting in their flourishing in drier years. In the fynbos, black wattle infestations are due to the species being was found to be more drought tolerant than native species (Crous *et al.*, 2012). Riparian ecosystems are particularly vulnerable to invasion, as flooding leaves disturbed areas that invasive alien plants can exploit (Richardson *et al.*, 2007). A survey of dragonfly (Odonata) species on the Red Data List found that all 12 species were threatened by invasive alien plants, largely due to shading and changes in vegetation structure (Samways & Taylor, 2004). Management of riparian ecosystems are critical to ensure consistent water supply for the country (Cullis *et al.*, 2007).

2.4.2 Invasive alien plant species of significance in South Africa

According to the Southern African Plant Invaders Atlas (SAPIA) database (2007), there are 600 alien plants listed in South Africa (Henderson, 2007). The most prolific and widely studied invasive alien plant species in South Africa are the Australian *Acacia* species, most notably *A. mearnsii* (black wattle), *A. cyclops* (red-eyed wattle) and *A. saligna* (Port Jackson wattle) (Henderson, 2007). All these species were originally introduced for silviculture in the early 1800s (Henderson, 2006, Bromilow, 2010) and all have had severe impacts across South Africa (Le Maitre *et al.*, 2011). Most of the impacts are as a result of high seed production, resulting in native plants being outcompeted for space (Le Maitre *et al.*, 2011). Dense infestations of *Acacia* trees result in water loss as these trees utilise high levels of water (Dye & Jarmain, 2004), resulting in soil erosion and further changes to vegetation (van der Waal *et al.*, 2012). Nel *et al.* (2004) identified invasive species that are widespread and abundant across South Africa such as *Acacia mearnsii*, *Populus alba*/*canescens* and *Prosopis* sp. The majority of the worst invaders in South Africa have large, widespread populations, and management of these species is very costly (Marais & Wannenburgh, 2008).

2.4.3 Emerging invasive alien plants in South Africa

South Africa has a growing number of invasive alien plants that are known as emerging invasive alien species (Carbutt, 2012). Emerging invaders are defined as species that currently have a low impact on South African ecosystems, but have the capacity to have a large impact in the future (Nel *et al.*, 2004). According to a study by Mgidi *et al.* (2007), 80% of South Africa is vulnerable to invasion by at least one emerging IAP, and thus these plants need attention by management authorities. A list of 84 emerging invasive alien plants in South Africa was compiled by Nel *et al.* (2004) in order to prioritise management requirements for these species. According to this list, half the emerging invasive alien plant species in South Africa are trees. As a result of the need for prioritised management of emerging species, the South African National Biodiversity Institute started a programme to detect and manage these species before the invasion become unmanageable (Wilson *et al.*, 2013).

2.5. Management and future perspectives of invasive alien plants in South Africa

South Africa is a leader in invasive alien plant control (Cronk & Fuller, 2001), and utilises a variety of tools in managing IAPs, such as biological control (Zimmermann *et al.*, 2004) and the well-known Working for Water programme (MacDonald, 2004). Management of invasive alien plants is written into legislation, with different categories for alien plants depending on their use and invasive potential (Bromilow, 2010). As invasive alien trees are of particular concern to South Africa due to their large consumption of water and widespread abundance, their management has been widely reviewed in the past (e.g. Le Maitre *et al.*, 2011, van Wilgen & Richardson, 2014).

South Africa has clear legislation regarding invasive alien plants and their control. The National Environmental Management: Biodiversity Act (NEM:BA) was officially gazetted as Act 10 of 2004. The purpose of the act is to provide guidelines for management of the environment with regards to species at risk of extinction and those that pose threats to the environment. Prior to this, invasive species were listed in the Conservation of Agricultural Resources Act (CARA), which was a list of plants that posed problems to agriculture (Act 43 of 1983). In 2009, a draft list with new species and up to date categorisations was published for comment. In 2014, the final draft of listed invasive species and prohibited species was published. The difference between the CARA list and the new NEM:BA list is that NEM:BA provides for new species to be added as the relevant authorities become aware of the problems that these species pose. On the CARA list, all new species were placed on a ‘suspect’ list, without further categorising them. This led to issues pertaining to the importation of new species, and removal efforts of species that were already residing in the country. Within the NEM:BA regulations, all species are categorised according to the potential for invasiveness, the size of the population and their use in industries such as forestry and agriculture. A list of definitions for the different categories is provided in Table 2.1.

Management of invasive alien species in South Africa is well known around the world through the Working for Water programme (MacDonald, 2004). The programme employs people from low income households in eradication efforts of invasive alien plants, with a focus on trees in riparian areas. The result is an increased streamflow, which is highest in areas where dense stands of IAPs had high transpiration levels (Dye & Jarmain, 2004). For example, Dzikiti *et al.* (2013) found that clearing of mesquite (*Prosopis* sp) in the Northern Cape resulted in groundwater savings of 70m^3 per month. Similarly, removal of pines (*Pinus* sp.) increased the responsiveness of catchments to rainfall events, decreasing flooding (Le Maitre *et al.*, 2014).

Biological control as a management tool in South Africa has had many success stories (Zimmermann *et al.*, 2004). One of the first attempts at biocontrol was of *Opuntia ficus-indica* and *O. monacantha* in the early 1900s using cochineal insects (Henderson, 2006), with both these species being reduced from pest status in a matter of decades. Seed-eating weevils as biological control to reduce seed numbers for invasive *Acacia* species has been used successfully, especially in the Western Cape (McConnachie *et al.*, 2012). This is an ideal method as many *Acacia* species are used in the forestry industry, and control through reduction of seeds prevents conflict between tree growers and conservationists (Donaldson *et al.*, 2014).

Clearing operations are not a ‘miracle cure’, requiring long term monitoring and occasionally active restoration to return the environment to a desired state (Le Maitre *et al.*, 2011). After assessing several removal methods, Blanchard & Holmes (2008) found that felling trees and removing the slash from the site resulted in the site returning closely to conditions prior to invasion. However, they did report that native vegetation cover was lower than reference sites and species composition was different. Clearing sites, especially of areas that were invaded by extremely invasive species, require regular monitoring and follow up clearings. Seeds remain stored in seed banks for many years, although there have been few studies in South Africa to determine how long these seeds remain viable (Ruwanza *et al.*, 2013). In the Cape Floristic Region, black wattle was still found in dense stands eight years after clearing (Pretorius *et al.*, 2008). This was because only one follow up had been done in the area after clearing. However, clearing does not necessarily have to include all trees, as Ruwanza *et al.* (2013) found that thinning trees by 40-50% had similar levels of recovery as sites that had been completely cleared of invasive alien plants. Clearing projects, especially those that involve the removal of trees, are often controversial (van Wilgen, 2012). Members of the public feel that removal of trees is counterintuitive to the drive for tree planting and that it is removing green spaces from the environment (van Wilgen, 2012).

It should be noted that management operations for invasive alien plants are difficult for a number of reasons. Budget constraints are the biggest problem to most successful clearing projects (Krug *et al.*, 2010). Clearing invasive alien plants are cheaper when invasions are small (Marais & Wannenburgh, 2008), but detecting invasive populations before they spread are very difficult and require monitors over large areas (Jacobs *et al.*, 2014). Bioclimatic envelopes can be used to determine whether an area is climatically suitable for a given species reducing the search area (Wilson *et al.*, 2007, Jeschke & Strayer, 2008, Bradley *et al.*, 2010, Jiménez-Valverde *et al.*, 2011). It is important to identify all possible areas that may be invaded to focus the search for IAPs in order to eliminate small populations (Kaplan *et al.*, 2014). However, Broennimann *et al.* (2007) found that the invasive population did not necessarily grow in climatically similar areas when compared with the native range of the plant species.

Commitment from politicians to environmental causes is also a confounding factor to clearing efforts, as many politicians are focussed on combating social problems rather than environmental ones (Roura-Pascual *et al.*, 2011). In many poor communities people rely on invasive alien species for survival. A study of invasive alien plant uses in rural communities in KwaZulu-Natal, de Neergaard *et al.* (2005) found that wattle trees are widely utilised for building, heating and income was generated through the sale of firewood. In Limpopo province, BaPedi traditional healers are using 35 exotic species as medicine to treat as many as 20 human ailments (Semenya *et al.*, 2012). There are costs and benefits to IAP use by rural communities. On the one hand, use of IAPs leads to lower use of indigenous species, but at the risk of allowing invasive species to populate over a large area (Semenya *et al.*, 2012).

Future management efforts should focus on maintaining the programmes that have already been started (Roura-Pascual *et al.*, 2011). In addition, management plans should also aim to reduce seed production by invasive alien species to help contain spread of invasive alien species (van Wilgen *et al.*, 2011). A plan to reduce the spread of seed along roadways should be attempted (Rahlao *et al.*, 2014), but will be difficult to implement. Research needs to be conducted on the life history of invasive species in South Africa *in situ*. Understanding their reproductive methods and how species spread can go a long way into creating focussed plan for clearing (Geerts *et al.*, 2013b). Early detection of invasive plant species is key to eliminating problem plants before the number of populations become too great to handle (Kalwij *et al.*, 2014).

2.6. Conclusions

Alien invasive plant species have become a feature of most ecosystems in South Africa. While there is no general set of plant traits that determine invasibility, invasive alien plant species do have some features in common. Traits include adaptations resulting in superior competitive abilities, self-compatibility and autonomous self-pollination, seed adaptations that promote dispersal and few enemies regulating populations. While many species of invasive alien plants are found in areas that share similar climatic conditions to the native range, this is not always true, as shifts in climatic niche can occur in the invaded range. There have not been many studies focussing on climate niche shifts of invasive alien plants in South Africa, and further research in this area is required. Furthermore, there are few studies of the effects of climate change on invasive alien species in South Africa. Certain habitats may be susceptible to invasion, especially when there is an abundance of resources that invasive alien species may be better able to exploit than native species. The impacts of invasive alien species on the biodiversity of South African ecosystems are always negative. Changes to nutrient cycles and hydrology of ecosystems drive the decline in native vegetation and the increase in invasive alien species. Faunal communities are also affected due to changes in vegetation structure and associated alteration of microclimatic conditions. Despite the negative impacts of invasive alien species, the outlook for South Africa is relatively positive. There is good legislation in place to curb the spread of invasive alien plants, as well as management of invasive alien trees through the Working for Water programme. Similarly, there has been successful use of biological control in the management of several invasive alien species.

However, clearing operations are a continuous process that requires dedication from managers and co-operation from government officials.

Table 2.1: Definitions of the different category listings for invasive alien species in South Africa as made in the National Environmental Management: Biodiversity Act (10 of 2004), published in Gazette 37320 in February 2014

Category	Definition
1a	Species requiring immediate control – so called 'emerging' weeds. These species have small populations that have a realistic chance of being eradicated e.g. *Cytisus scoparius* (Scotch Broom)
1b	Species that need to be contained. These species have populations that are too large to eradicate, thus control efforts must be made to reduce their spread e.g. *Chromolaena odorata* (Triffid weed/ Chromolaena)
2	Species that require a permit to carry out restricted activity within a specific area. Species in this category are usually timber trees and plants that are used in agriculture that have invasive traits e.g. *Acacia mearnsii* (Black wattle)
3	Species that are subject to exemptions. These are species that have some cultural or historical significance and are allowed to remain where they currently are, but no new individuals of the species may be introduced e.g. *Melia azedarach* (Seringa)

Chapter 3

Evidence of self-compatibility in the invasive alien plant *Hypericum pseudohenryi* in South Africa

ABSTRACT

Plants that are capable of uniparental reproduction or are self-compatible are considered to be more likely to be successful at colonising new regions due to their ability to establish populations with a single propagule. Self-fertilisation comes at the risk of inbreeding depression, which results in progeny with reduced fitness. Many invasive alien plants do not, however, seem to be affected by inbreeding depression. The breeding system and performance of selfed versus crossed progeny was investigated in *Hypericum pseudohenryi* (Hypericaceae) an emerging invasive alien plant in South Africa. Experiments were conducted at three sites in the invasive range of *H. pseudohenryi* in KwaZulu-Natal, South Africa and seeds resulting from field experiments were germinated in the lab. The proportion of seeds germinating from seeds of hand cross-pollinated flowers was significantly higher than seeds of self-pollinated and open flowers, indicating that *H. pseudohenryi* is self-compatible in the invasive range. Hand self-pollinated flowers had significantly higher seed set than those set solely through autogamy, indicating that the species is pollinator dependent. *Hypericum pseudohenryi* did experience inbreeding depression in the studied populations, but further testing across the introduced range is needed to determine if inbreeding depression is prevalent in South Africa.

3.1. Introduction

Baker (1955) proposed that plants capable of uniparental reproduction would be most successful in establishing populations in new environments. Capacity for self-fertilisation is considered one of the most important characteristics of plants that are invasive (Richardson *et al.*, 2000, Cronk & Fuller, 2001). The capacity for an invasive alien plant to self-fertilise allows populations in the new environment to increase in numbers rapidly from a single propagule without the need for specialised pollinators (Cousens & Mortimer, 1995, Burns *et al.*, 2011). Not all invasive alien plants are self-compatible in their native range, but may acquire self-compatibility as a result of genetic mutations that enable populations to successfully reproduce despite low plant density in the new environment (Petanidou *et al.*, 2012). The reliance on self-fertilisation for seed set is known as reproductive assurance (Eckert *et al.*, 2009). Self-pollination can also reduce the effects of pollen limitation by providing an additional source of pollen, thus ensuring a high seed set per flower (Rambuda & Johnson, 2004).

Despite conferring reproductive assurance, self-fertilisation can come at the cost of reduced fitness of progeny, known as inbreeding depression (Eckert *et al.*, 2009). Selfing results in the loss of genetic variability in the population due to increased homozygosity in the majority of individuals within the population (Charlesworth & Charlesworth, 1987). When genetic load is present, the resulting offspring are typically less fit for the environment and local extinction can occur when environmental conditions change (Charlesworth & Charlesworth, 1987). In spite of this risk, many invasive alien plants show very low levels of inbreeding depression in their populations (Pujol *et al.*, 2009, Rodger *et al.*, 2013). Self-pollination may reduce the frequency of deleterious genes in the source population resulting in offspring from phenotypes that are tolerant of the new environment (Ronce *et al.*, 2009, Levin, 2010). This ensures that the extinction threshold in a small population is eliminated, allowing the population to establish and increase with time (Morgan *et al.*, 2005). The production of seeds through sexual reproduction allows the population to increase and larger areas to be colonised through seed dispersal than asexual plant reproduction (Burns *et al.*, 2011).

Invasive alien plants are a threat to biodiversity worldwide, due to their ability to create large populations at the expense of the natural vegetation (Dukes & Mooney, 1999, Mack *et al.*, 2000). The production of large quantities of seed results in dense stands of the invasive alien plant taking over the landscape (Iponga *et al.*, 2009a, Geerts *et al.*, 2013a). A study by van Kleunen & Johnson (2007) found that self-compatible invasive alien plants have larger invaded ranges than self-incompatible plants. Self-compatibility in some invasive plants may be as a result of artificial selection for self-compatible plants in the ornamental trade to increase production (Rambuda & Johnson, 2004). It is not surprising then that many invasive alien plants that were established in South Africa were introduced for the ornamental trade (Richardson & Rejmánek, 2011).

Hypericum pseudohenryi N. Robson is an invasive alien plant in South Africa that threatens biodiversity in the uKhahlamba-Drakensberg region, known for its pristine habitats (Carbutt, 2012). It is thought that *H. pseudohenryi* was originally brought into South Africa as an ornamental plant, possibly as early as the 1950s (Bromilow, 2010). *Hypericum pseudohenryi* grows along river banks and dry slopes at high altitudes, forming dense stands and eliminating native plants (Carbutt, 2012). The success of *H. pseudohenryi* as an invader is believed to be due to its ability to self-pollinate and produce large numbers of small seeds (I. Nänni, pers. comms). As *H. pseudohenryi* is considered an “emerging” invader in South Africa, and is not known to be invasive elsewhere in the world, very little research has been conducted on the species and its invasive traits. Within the genus *Hypericum*, there are several different modes of reproduction. Within the section Ascyreia, to which *H. pseudohenryi* belongs (Robson, 1985), some species undergo sexual reproduction, while other species can be facultative apomicts (Matzk *et al.*, 2003).

In this study, the reproductive ecology of *H.* pseudohenryi was documented in two components. First, the breeding system of *H. pseudohenryi* was tested with field experiments. Secondly, seeds resulting from different pollination treatments were germinated in the lab to determine germination rates and to establish if frost conditions play a part in germination. The main questions addressed in this study are: 1) is *H. pseudohenryi* self-compatible and 2) does *H. pseudohenryi* experience inbreeding depression in its invasive range in South Africa.

3.2. Methods

3.2.1 Study species

Hypericum pseudohenryi is a perennial shrub that grows up to 1.7m tall, and originates from Yunnan and Sichuan provinces in China (Robson, 1985). Usually found in forest areas as well as grassy slopes, *H. pseudohenryi* has become invasive in South Africa in the KwaZulu-Natal Midlands, the UKhahlamba Drakensberg and the mountainous areas of the Eastern Cape. It grows at altitudes ranging from 1400-3800m above sea level (Robson, 1985).

Flowering occurs during summer (Late October – January in South Africa) commencing after the start of the summer rain. Each bush produces many large yellow flowers (30-55mm diameter) with as many as 40 showy stamens on each flower. The flower produces no nectar, but rather offers a pollen reward to pollinators. The flowers are visited by generalist pollinator species, notably flies, honey bees and beetles (pers. obs.). Flowers produce up to 500 small (15-20mm long) brown seeds in a dry capsule which opens to release seeds between April and May.

3.2.2 Study sites

The study began in December 2013 and continued until January 2015. Three study sites were chosen in Kwa-Zulu Natal, South Africa: Giant’s Castle (29°15'29"S 29°31'49"E; 1780m a.s.l.), Monk’s Cowl (29°02'55"S 29°24'25"E; 1480m a.s.l) and Mbona Private Game Reserve (29°17'38"S 30°21'08"E; 1350m a.s.l.). Giant’s Castle was only used in the 2013-2014 season, as flowering occurred very late in the season during the 2014-2015 season. At Mbona Private Game Reserve, *H. pseudohenryi* was found in dry grassland alongside the road and on the edge of the forest. *Hypericum pseudohenryi* at Monk’s Cowl grew along the road and down a slope towards a river. Giant’s Castle *H. pseudohenryi* plants grew alongside the road, growing up a very steep slope that had a spring rising from the top.

3.2.3 Breeding system

To prepare for tests for self-compatibility, flowers on ten plants of *H. pseudohenryi* were bagged while in bud. The following day, the bags were removed from flowers which were treated with either self-pollen by hand (Hand self), cross pollen with pollen from a plant at least 20m away (Hand cross), or were emasculated and left open (Open emasculated). The open emasculated treatment was to test whether pollinators were contributing to seed set. One flower on each plant remained bagged for the following week to prevent insect activity to test for autogamy (Bagged self). As a control, a flower that had not been bagged and was not manipulated was marked on each plant (Open). Seed set was used as an indicator of reproductive output, as all flowers set fruit.

Hand self-pollinated treatments were undertaken in the 2014-2015 season only. To test whether there was a difference in seed production across the season, in the 2014-2015 season, all five treatments were done on ten plants each month from November through to January at each site. In April following the flowering season, the dry capsules were removed from the plants just prior to maturation.

To control for the repeated measures of seed set in flowers from the same plant, Generalised Estimating Equations were used to analyse the data on SPSS version 23 (IBM, 2015), using a negative binomial with log link function and exchangeable correlation matrix. A pairwise contrast was used to compare means, and sequential Sidak adjustments were made for multiple comparisons. All means were computed for the linear predictor and then back transformed.

3.2.4 Germination of seeds

As *H. pseudohenryi* grows in areas where frost regularly occurs, seeds were frozen for a period prior to the germination experiment. Ten seeds from each of the four pollination treatments (autogamous, open emasculated, open and hand cross-pollinated) from each site of the 2013-2014 season were frozen for 0h, 1h, 3h, 6h and 12h. Once the seeds were removed from the freezer, they were sterilised by immersion in a 70% ethanol solution for 30s. Seeds were then immersed in a 53% aqueous solution of 5.2% sodium hypochlorite in water with one drop of Tween 20 per 500mL for 20 min and finally rinsed three times with distilled water. Once sterilised, seeds were placed on agar plates with a Murashige and Skoog medium. Sealed agar plates were positioned in a controlled climate growth room, with temperature maintained at 25°C and 12h cycles of light. The number of seeds that germinated per agar plate was recorded every 5 days for 45 days.

Generalised Estimating Equations were used to analyse the proportion of seeds germinated on SPSS version 23 (IBM, 2015), using a gamma distribution with log link function and exchangeable correlation matrix. A pairwise contrast was used to compare means for pollination treatments and site, while a simple contrast using 0h as a reference was used for the freezing treatments. Sequential Sidak adjustments were made for multiple comparisons. All means were computed for the linear predictor and then back transformed.

3.3. Results

3.3.1 Breeding system

The number of potentially viable seeds produced per flower differed greatly across treatments (Fig. 3.1). For all sites, across both seasons, there was no significant difference in seed set between open emasculated and autogamous flowers (p=0.931). There was no significant difference in seed set between the hand self-pollinated flowers and the hand cross-pollinated flowers (p=0.931) nor between the hand self-pollinated flowers and the open flowers (p=0.891). However, there was a significant difference in seed set between the hand cross-pollinated and open flowers (p=0.001). There was also a significant difference in seed set between the open emasculated flowers and autogamous flowers compared to the other three treatments.

Of the three study sites for the open treatment (Fig. 3.2), Giant’s Castle had the highest seed production per flower and Monk’s Cowl had the lowest ($p=0.001$; $\chi^2=37.047$). At the site level (Fig. 3.3), Giant’s Castle had a significantly higher number of seeds per flower for autogamous flowers compared to the other sites (p=0.001). None of the treatments at Giant’s Castle had significantly different seed sets from each other. Flowers at Mbona Game Reserve followed the general trend most closely, with open, and cross-pollinated and hand self-pollinated flowers significantly different in the number of seeds produced from the autogamous and open emasculated treatments. Open flowers at Monk’s Cowl had a significantly higher seed set compared to autogamous flowers (p=0.001), open emasculated (p=0.001), hand cross-pollinated (p=0.001) and hand self-pollinated flowers (p=0.005).

There were differences in the number of seeds produced per flower for open treatments across the season (Fig. 3.4). There was a higher seed set per flower in December (mid-season) compared to November (early season; p=0.008) and January (late season; p=0.001). There was no significant difference in seed set between November and January (p=0.186).

3.3.2 Germination of seeds

In Fig. 3.5, seeds from hand cross-pollinated flowers had a higher proportion germinating compared to seeds from flowers tested for autogamy (p=0.30), open (p=0.32) and open emasculated (p=0.47). Freezing the seeds had no significant difference on the proportion of seeds that germinated (Fig. 3.6; p=0.204). Seeds originating from the Monk’s Cowl site (Fig. 3.7) had a significantly higher proportion germinating compared to the Giant’s Castle (p=0.33) and Mbona (p=0.42) sites.

3.4. Discussion

3.4.1 Breeding system

The results show that *Hypericum pseudohenryi* is self-compatible, which is consistent with Baker’s Law (Baker, 1955), but is pollinator dependant. Flowers were able to set seed when caged, but had a significantly higher seed set when self-pollinated by hand (Fig. 3.1). Hand cross-pollinated flowers produced similar numbers of seeds to the hand self-pollinated flowers (Fig. 3.1), which indicates that the population is likely to have a mixed mating system. Flowers of *H. pseudohenryi* were not pollen limited, as the unmanipulated open flowers had a significantly higher seed set than cross-pollinated flowers (Fig. 3.1). Self-compatibility in invasive alien plants may help ease pollen limitation in the introduced range (Rambuda & Johnson, 2004).

Seed sets were lower at Mbona and Monk’s Cowl compared to Giant’s Castle (Fig. 3.2). According to Robson (1985), *H. pseudohenryi* is found at altitudes of 1400m to 3500m in the native range. The Mbona population (1350m) and Monk’s Cowl population (1480m) are at the lower end of the altitudinal range for *H. pseudohenryi*, while Giant’s Castle (1780m) is firmly within the range. The higher seed set could be due to more optimal climatic conditions prevailing at Giant’s Castle than the other two sites. Giant’s Castle also had a high seed set for self-pollinated plants (Fig. 3.3), which could indicate that the population at Giant's Castle has adapted to low pollinator presence compared to the other two sites (pers. Obs.).

Seed production was highest in the middle of the flowering season (December, Fig. 3.4). Temperatures during December were just under 20°C for all sites, and had an average rainfall of 155mm. November was slightly cooler and drier, while January was hotter and wetter. The mid-season high seed production could indicate that the conditions in December provide were optimal for seed production.

One of the most important characteristics of an alien invasive plant (IAP) is the potential to produce seeds in the absence of pollinators. For this, self-compatibility, and the ability for autonomous self-pollination (Cronk & Fuller, 2001) are therefore important conditions in order to maintain populations through reproductive assurance (Levin, 2010). Other studies of invasive alien plants in South Africa have found similar results to those found in this study. In a study of 17 other invasive alien plants in South Africa Rambuda & Johnson (2004) found that all 17 IAPs were self-compatible in South Africa. Burns *et al.* (2011) found that introduced species were more likely to be autogamous than native species in the community, and that introduced species were more likely to reproduce sexually than asexually. Sexual reproduction could create fitter progeny in introduced plants, increasing the likelihood of survival in a new environment (Cousens & Mortimer, 1995). Self-pollination in small populations can reduce the extinction threshold of species by increasing the number of individuals, even though the progeny of selfing may not be as fit as outcrossed progeny (Morgan *et al.*, 2005).

Not all studies have found introduced species to be self-compatible, as introduced species are not always perfectly self-compatible or self-incompatible, even in their native ranges (Petanidou *et al.*, 2012). Murren & Dudash (2012) found that *Mimulus guttatus* populations outside of their native range had reduced rates of sexual reproduction. This could be due to a lack of suitable pollinators in the introduced range. In the case of this study, *H. pseudohenryi* was visited by many different pollinators, including flies, bees and beetles (pers. obs.). One possible reason that the open emasculated flowers had such low seed set, despite the high number of available pollinators, is that the flowers were no longer rewarding and thus lost their attractiveness to pollinators. Furthermore, an important assumption when doing breeding experiments on flowers is that emasculation of the flower does not decrease the rate of outcrossing by pollinators through flower damage or altering flower attractiveness (Eckert *et al.*, 2009). However, pollinators might be sensitive to changes in flower morphology, resource availability, or floral scent emission (e.g. physiological stress due to damaging the flowers).

As *H. pseudohenryi* is used as an ornamental plant, it is possible that plants brought into South Africa had an artificially high rate of selfing. Ornamental flowers that have high seed sets are often favoured in cultivation to increase propagation by horticulturists (Rambuda & Johnson, 2004). Initial populations brought into South Africa for the plant industry would have to have been sustained through seed production as *Hypericum* species are known not to grow readily from cuttings (Crockett & Robson, 2011).

3.4.2 Germination of seeds

In this study, the proportion of seeds germinated from cross-pollinated flowers was significantly higher than the proportion of seeds germinating from other treatments (Fig. 3.5), indicating that inbreeding depression may be occurring in the populations as a result of selfing. Freezing the seeds prior to germination had no effect on the germination of seeds (Fig. 3.6), which suggests that frost may not be as important a factor as was expected. Monk’s Cowl had the highest proportion of seeds germinating of the three sites (Fig. 3.7), which was surprising as it had the lowest seed set per flower of the three sites (Fig. 3.2).

There are mixed conclusions about inbreeding depression in invasive alien plants. Most studies find that there is decreased inbreeding depression in IAPs (e.g. Pujol *et al.*, 2009, Murren & Dudash, 2012, Rodger *et al.*, 2013). Some theorise that inbreeding may result in reduced genetic variability but as a result of reduced variance, inbreeding depression may then decrease (Ronce *et al.*, 2009). It is intuitive that reduced inbreeding depression in IAPs would explain their success in colonising new habitats. Although there is evidence that *H. pseudohenryi* has inbreeding depression, the number of seeds germinating from seeds of the hand cross-pollinated treatment was only slightly more significant than the other treatments. Despite the low seed set in flowers from the Monk’s Cowl site, it had the highest proportion of seeds germinating. This could be as a result of increased maternal resource allocation to the seeds as there were fewer in each fruit.

3.4.3 Future directions

Further research on the breeding system could be done on the extreme margins of the invasive population of *H. pseudohenryi* in South Africa. There are a few plants that have been found far out of the normal altitudinal range of *H. pseudohenryi*, including one plant found as low as 670m a.s.l.

This could help determine whether *H. pseudohenryi* has the potential to spread into areas with suboptimal conditions for reproduction and growth. The KwaZulu-Natal populations of *H. pseudohenryi* may have been introduced more recently than populations found in the Eastern Cape region, with herbarium records suggesting that *H. pseudohenryi* has been in the Eastern Cape since the early 1950s. Studies of the breeding systems of these populations may yield interesting results when compared to the newer population of KwaZulu-Natal.

3.5. Conclusions

Hypericum pseudohenryi fulfils Baker's Law for introduced plants in that it is capable of uniparental reproduction (Baker, 1955), but it is pollinator dependant. However, it does not experience pollen limitation within the studied populations, possibly due to the high rate of self-compatibility. There was evidence of inbreeding depression in the studied populations of *H. pseudohenryi* in South Africa, which contrasts that of other studies of IAPs.

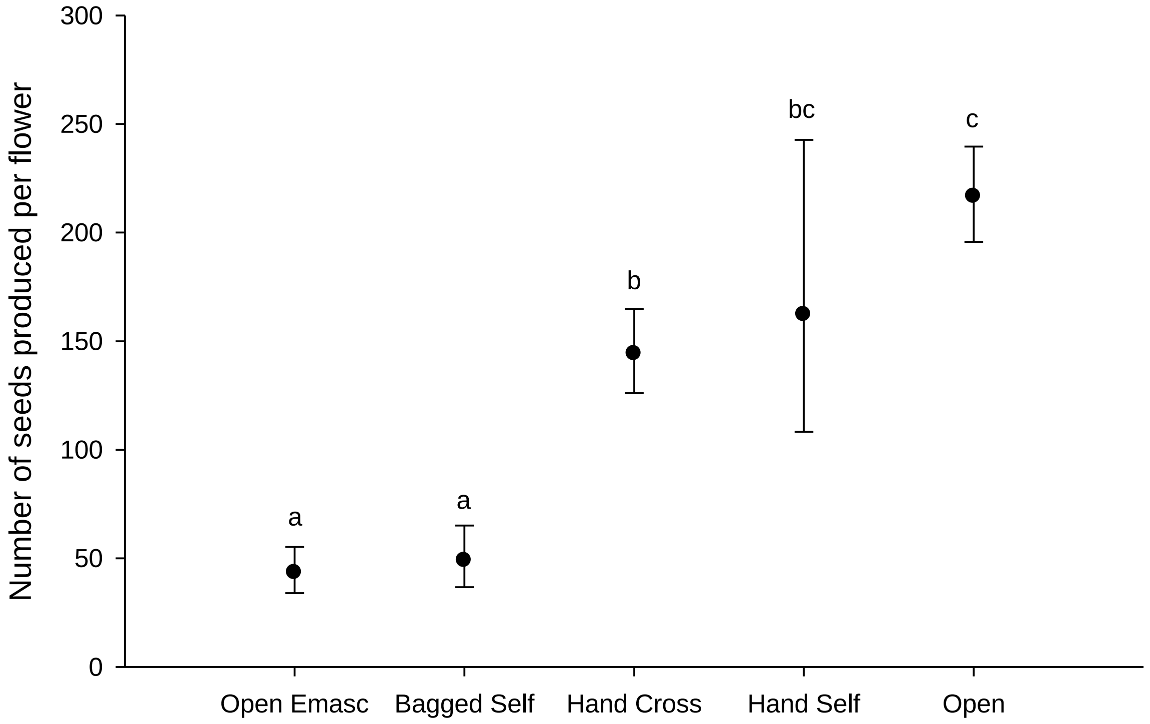

Fig. 3.1. The number of seeds produced (±SE) per flower for five pollination treatments at three study sites (Giant's Castle, Monk's Cowl and Mbona Nature Reserve): open emasculated flowers (Open Emasc), autogamous flowers (Bagged Self), hand cross-pollinated flowers (Hand Cross), hand self-pollinated flowers (Hand Self) and open flowers (Open). $p=0.001$; $\chi^2=271.611$. Means that share the same letter are not significantly different.

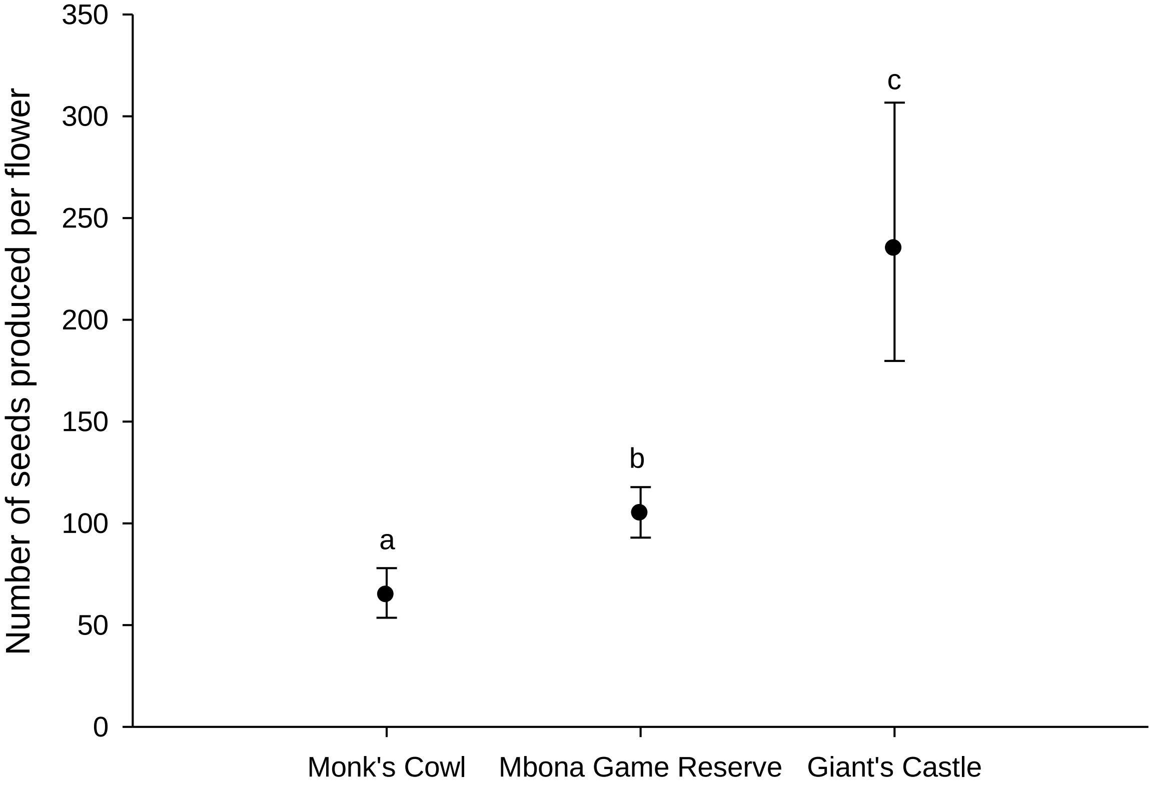

Fig. 3.2. The number of seeds produced (±SE) per flower for open treatments for the three study sites: Monk's Cowl (1480m), Mbona Nature Reserve (1350m) and Giant's Castle (1780m). $p = 0.001$; $\chi^2 = 37.047$.

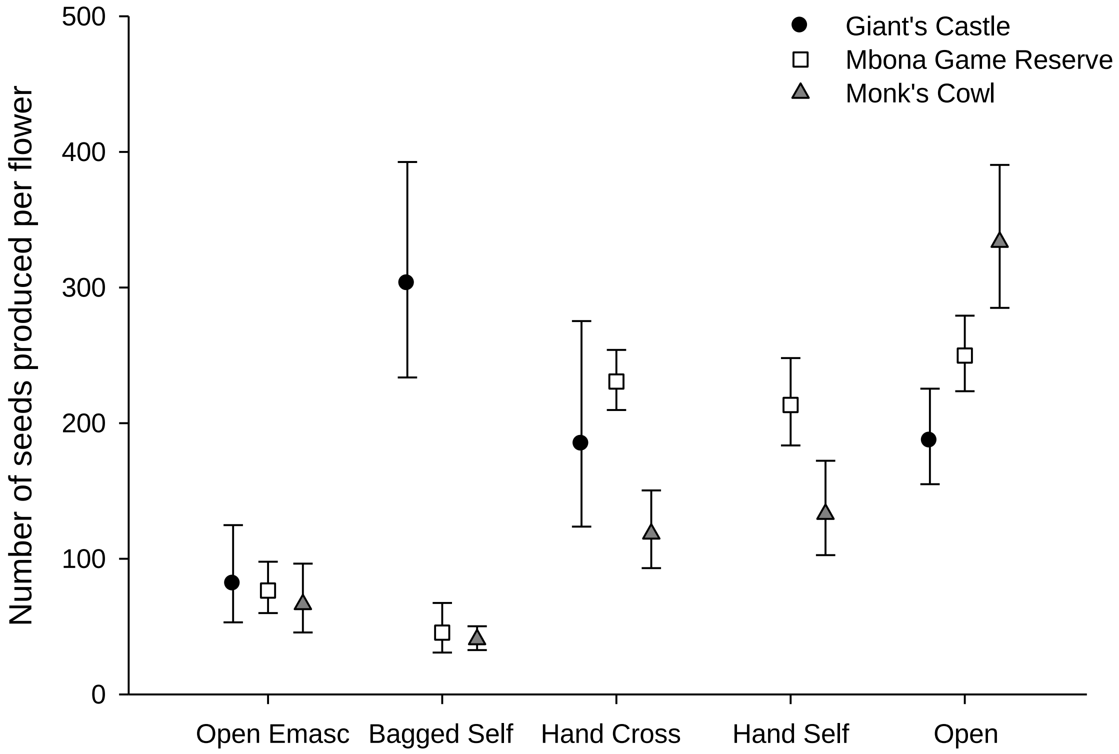

Fig. 3.3. The number of seeds produced (±SE) per flower for five pollination treatments (bagged flowers (Bagged Self), open emasculated flowers (Open Emasc), open pollinated flowers (Open), hand cross-pollinated flowers (Hand Cross), hand self-pollinated flowers (Hand Self)) for the three study sites: Monk's Cowl (1480m), Mbona Nature Reserve (1350m) and Giant's Castle (1780m).

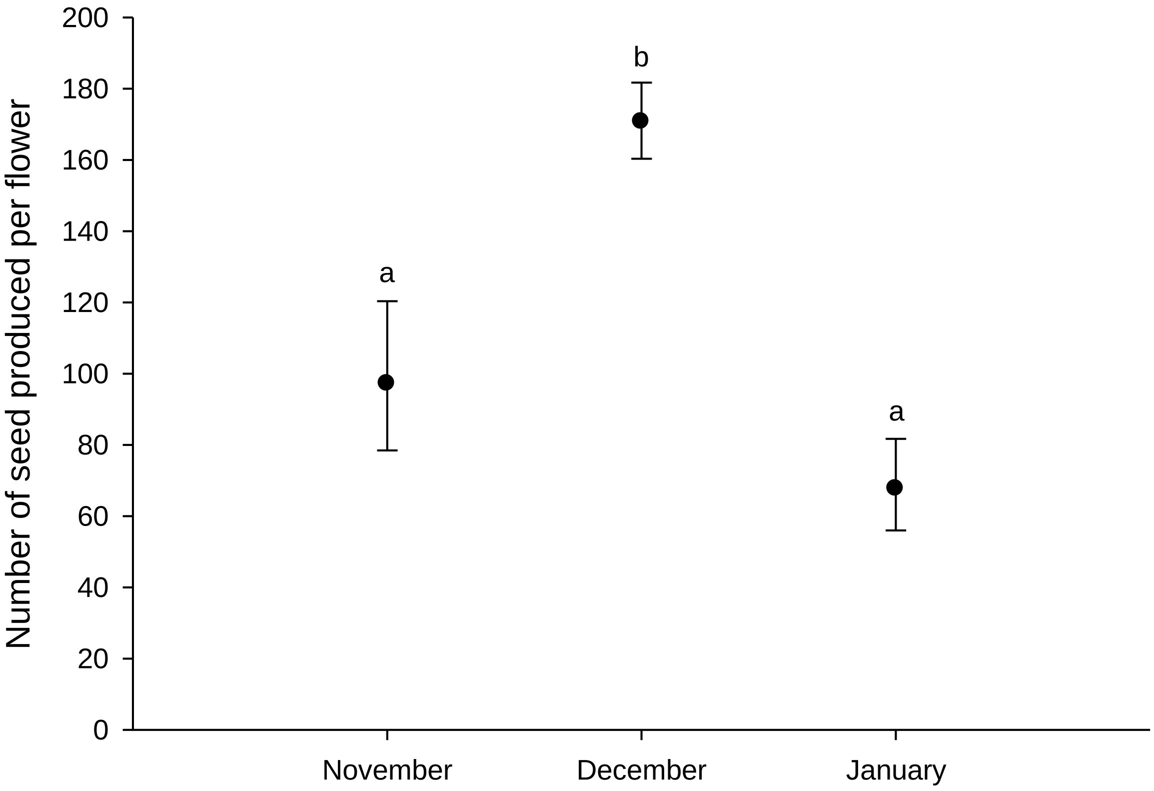

Fig. 3.4. The number of seeds produced (±SE) per flower for open treatments across the flowering season: November (early season), December (mid-season) and January (late season). p=0.001; χ^2=25.806. Means that share the same letter are not significantly different.

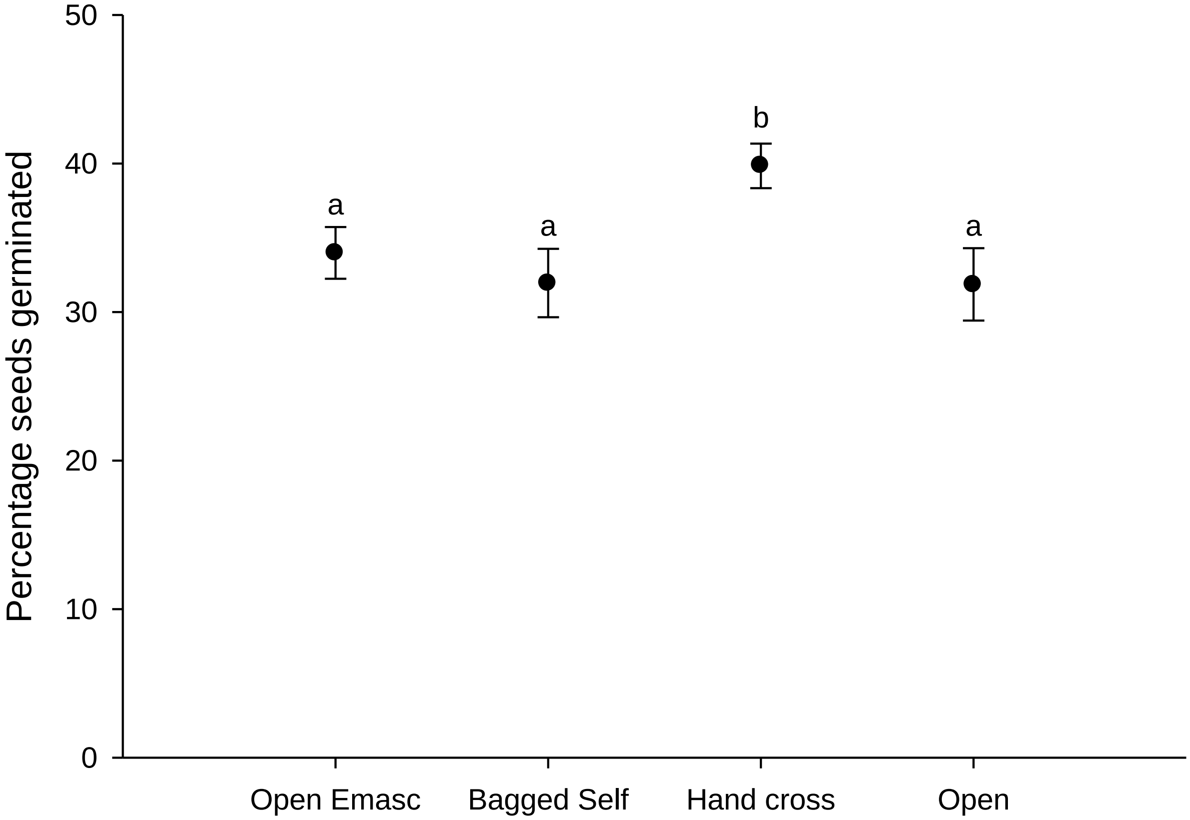

Fig. 3.5. The percentage (±SE) of seeds that germinated for four pollination treatments: Self-pollinated flowers, open flowers, open emasculated (Open Emasc) flowers and hand cross-pollinated (Hand cross) flowers. $p=0.004$; $\chi^2=13.345$. Means that share the same letter are not significantly different.

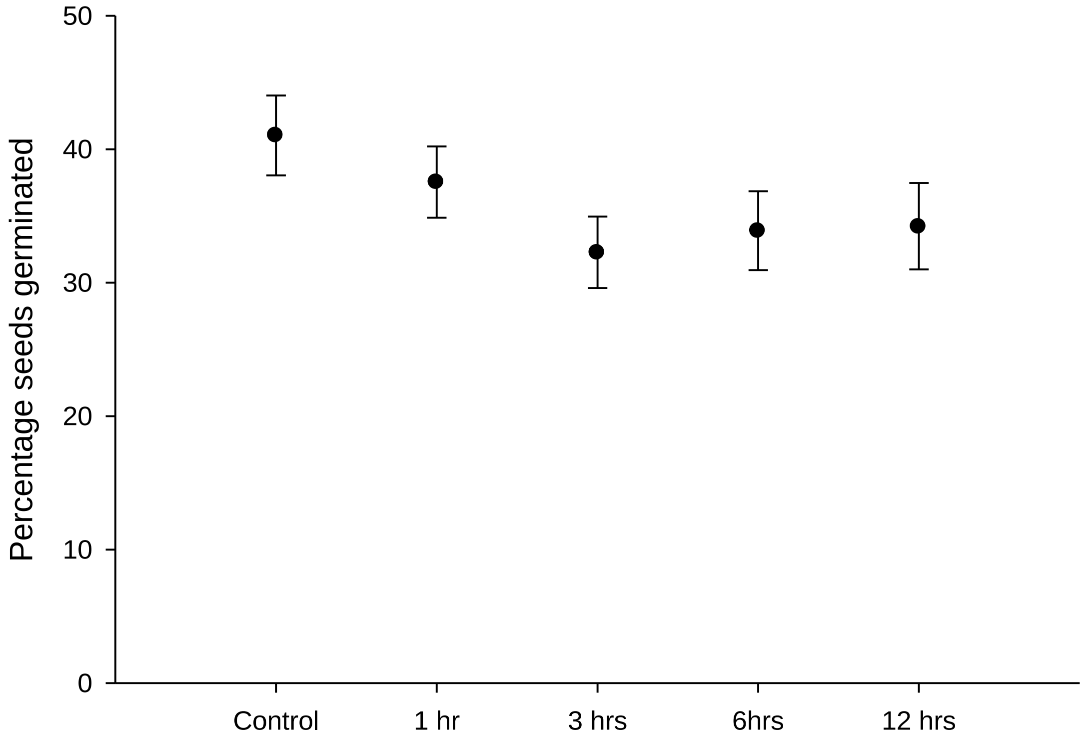

Fig. 3.6. The percentage (±SE) of seeds that germinated after being frozen prior to germination. Seeds were frozen for 0hrs, 1hr, 3hrs, 6hrs and 12hrs to simulate natural frost events. $p=0.204$; $\chi^2=5.938$.

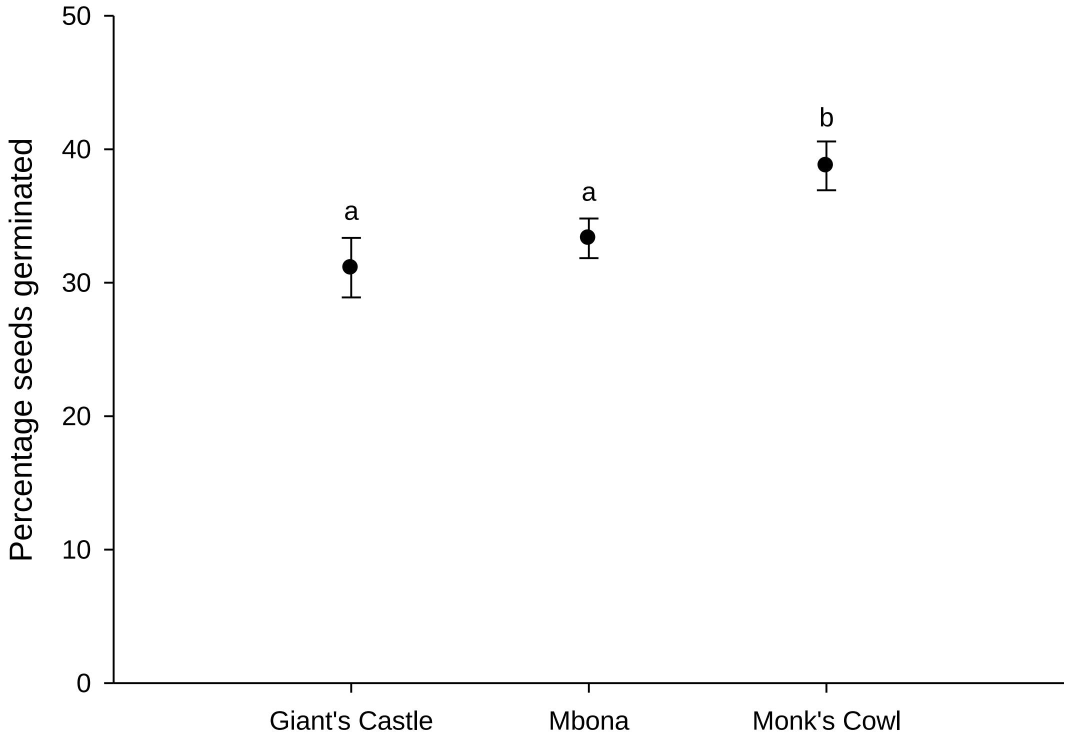

Fig. 3.7. The percentage (±SE) of seeds that germinated for three study sites: Giant's Castle (1780m), Mbona Nature Reserve (1350m) and Monk's Cowl (1480m). $p=0.17$; $\chi^2=8.147$. Significant differences are indicated by different letters.

Chapter 4

Modelling the climatic niche of the invasive alien plant *Hypericum pseudohenryi* in South Africa under current and future climatic conditions

ABSTRACT

Invasive species are a global problem and are predicted to become increasingly prevalent with climate change. Predicting climatically suitable habitat of invasive alien species of concern can help manage species in the introduced range. Climate modelling is one of the tools used to predict range changes of species under different climate change scenarios. *Hypericum pseudohenryi (*Hypericaceae) is an invasive plant in South Africa, thought to have been imported for ornamental trade, from China. It has invaded many of the cooler areas in eastern South Africa. A database of coordinates for individual *H. pseudohenryi* plants in South Africa was developed and discrete populations were identified. Data from the Global Biodiversity Information Database was used to identify populations in the native range in China. Using future climate data modelled by the Hadley Centre, a model was created using MaxEnt to predict the distribution of *H. pseudohenryi* for current climatic conditions, using data from both the native Chinese range and the invaded range in South Africa. To model the distribution under future conditions, two different representative concentration pathways of greenhouse gasses were used to make predictions for 2050 and 2070. The model for current climatic conditions using data from the South African range shows that *H. pseudohenryi* has not yet realised its full extent in South Africa. Using the data from the native range does not result in an accurate prediction of areas with suitable habitat for *H. pseudohenryi* in South Africa. As *H. pseudohenryi* appears to require cooler temperatures, results indicate that with increasing temperatures as the climate changes over the next 60 years, the range of suitable habitats of *H. pseudohenryi* will contract. However, suitable areas for growth and reproduction fall within many pristine areas in the Drakensberg mountain range. It is suggested that management of *H. pseudohenryi* should focus on populations that are already at higher elevations to reduce the chance of *H. pseudohenryi* spreading into pristine areas at high altitudes

4.1. Introduction

Invasive alien plants are a serious threat to ecosystems throughout the world (Mack *et al.*, 2000). Invaders affect the structure and function of ecosystems by altering water regimes (Le Maitre *et al.*, 2002), nutrient cycling (Ehrenfeld, 2003) and displacing native species (Kohli *et al.*, 2004). Effective management of invasive alien plants requires monitoring of areas where the species is present to remove plants before dense stands occur (Bradley *et al.*, 2010). An effective tool in predicting areas that are at risk of invasion from exotic species is climate niche modelling (Peterson, 2003, Rouget *et al.*, 2004, Thuiller *et al.*, 2005, Beaumont *et al.*, 2009b). Plant ranges are often determined by climatic conditions, and are thus used to identify potential areas where invasive alien species occurs (Richardson & Thuiller, 2007, Kaplan *et al.*, 2014). Climate niche modelling uses known locations of a species and identifies corresponding areas with similar climatic conditions (Jeschke & Strayer, 2008). The model predictions identify the fundamental niche of the plant species in the invaded range, which may include areas that are not yet occupied by the species (Dullinger *et al.*, 2009).

As climates change with increases in carbon dioxide and other greenhouse gasses, it is expected that plant ranges will shift into new areas that have previously been unoccupied by that species (Dukes & Mooney, 1999). Climate change will result in shifts of plant species to areas that were previously climatically suitable (Beaumont *et al.*, 2009a). Many invasive alien plant species are expected to undergo range expansion as new areas become climatically suitable (Bradley *et al.*, 2010). However, some species may experience range contractions as areas become climatically unsuitable (Richardson *et al.*, 2010). Species that are adapted to colder climates are expected to retreat to higher altitude areas as increasing temperatures negatively affect these species (Parker-Allie *et al.*, 2009). Range shifts will occur for species that have efficient dispersal mechanisms and are thus able to migrate into new climatically suitable areas. Climate niche models are employed to predict possible shifts in climatically suitable habitats for invasive alien species under climate change (Jeschke & Strayer, 2008).

Several studies have shown that invasive alien plants sometimes undergo a climate niche shift in the invaded range and are able to successfully colonise areas that are climatically unsuitable in the native range (e.g. Broennimann *et al.*, 2007, Beaumont *et al.*, 2009b). Modelling data obtained in the native range may result in the climate niche of the invaded range being underestimated, resulting in failure to predict the invaded range (Welk, 2004). Climate niche shifts are suggested to result from release of the species from geographic constraints found in the native range (Beaumont *et al.*, 2009b), or as a result of release from enemies such as herbivores or pathogens (Broennimann *et al.*, 2007). Species that have been introduced to a region on several different occasions from different locations will have increased genetic diversity, allowing species to tolerate novel climate regimes (Lavergne & Molofsky, 2007).

Emerging invasive alien plants are species that have small naturalised populations still in the early stages of invasion (Mgidi *et al.*, 2007). An emerging invasive alien plant species, *Hypericum pseuodhenryi* (Family Hypericaceae) has been identified in the Drakensberg and KwaZulu-Natal Midlands (Carbutt, 2012). It is believed that *H. pseudohenryi* was introduced from China as an ornamental (Bromilow, 2010). As *H. pseudohenryi* is self-compatible (Chapter 3), with each plant able to produce hundreds of thousands of seeds per year, it is able to create dense stands across the landscape. *Hypericum pseudohenryi* threatens biodiversity in high altitude grasslands and riverbanks in the KwaZulu-Natal Drakensberg and Midlands areas, which are rich with endemic plant species (Carbutt, 2012). As *H. pseudohenryi* has not yet naturalised across the whole region of South Africa, it is important to identify areas of potential invasion by the species to inform management plans (Kaplan *et al.*, 2014).

As *Hypericum pseudohenryi* poses a threat to biodiversity in South Africa, the aims of this study were: 1) determine the climate niche of *H. pseudohenryi* in South Africa, 2) identify differences in climate niche in South Africa using data from native versus invaded range, 3) establish the expected range of *H. pseudohenryi* under future climatic conditions using different predicted scenarios.

4.2. Materials and Methods

4.2.1 Study species

Hypericum pseudohenryi is a perennial shrub that grows up to 1.7m tall, and originates from Yunnan and Sichuan provinces in China (Bromilow, 2010). Usually found in forest areas as well as grassy slopes, *H. pseudohenryi* has become invasive in South Africa in the KwaZulu-Natal Midlands, the UKhahlamba Drakensberg and the mountainous areas of the Eastern Cape (Carbutt, 2012). In the invaded range, *H. pseudohenryi* is self-compatible and is able to reproduce autogamously, resulting in dense thickets especially along river banks. It grows at altitudes ranging from 1400-3800m above sea level. Typically, *H. pseudohenryi* is found in areas with good summer rainfall, when flowering occurs, and cold winters (Robson, 1985).

4.2.2 Climate niche modelling

As invasive plant species are known to undergo climatic niche shifts (Broennimann *et al.*, 2007), naturalised plant records were used for the climate niche model as well as records from the native range in China. South African naturalised populations were identified through surveys in protected areas of KwaZulu-Natal in 2006, with records being made for individual plants (I. Rushworth, Pers. comm.). Between 2012 and 2013, plants cleared by contractors on agricultural land in the KwaZulu-Natal Midlands were recorded (N. Mthimikhulu, Pers. comm.). Naturalised populations of *H. pseudohenryi* were surveyed in the Eastern Cape in 2014 with localities derived from herbarium specimens. From all the recorded plants, 27 discrete populations were identified in South Africa for use in the climate niche model. For populations in the native range, records of population were compiled using the Global Biodiversity Information Database. Only records from China were used and 20 populations were identified for use in the climate niche model.

Five climatic variables were chosen based on observed climatic preference of warm, wet summers and cold winters. The climate data were obtained from WorldClim (ver. 1.4, Hijmans *et al.*, 2005). Climate variables used were: Annual mean temperature, temperature of the coldest quarter, annual precipitation, precipitation in the warmest quarter and precipitation in the wettest quarter. For future climate models the same model was used as for the current climatic data. Two predicted scenarios for 2050 and 2070 were selected from HadGEM2-AO database at a resolution of 30 seconds. The predicted scenarios are two of four representative concentration pathways (RCP), which are trajectories of future greenhouse gas atmospheric concentrations accepted by the Intergovernmental Panel on Climate Change (IPCC).

Scenario RCP 2.6 is the most optimistic of the four pathways, predicting that greenhouse gas emissions are currently reaching a peak, and will decline in the future. The predicted increase in global temperature for scenario RCP 2.6 is 1°C by 2070. Scenario RCP 6.0 is the most realistic considering current climate trends, which predicts that greenhouse gas emissions will reach a peak in 2080 and will result in worldwide warming of 2.2°C by 2070.

The climate niche modelling was run using MaxEnt (Phillips *et al.*, 2006). As absence data were not available for the study, background points were used in their place, resulting in the maximum area under the receiving operator curve (AUC) that could be achieved being >1 (Phillips *et al.*, 2006). The model was calibrated using 80% of the data and evaluated using the remaining 20% of the data. Thirty replicates of each model were run and an average from the replicates generated.

4.3. Results

4.3.1 Distribution under current climatic conditions

This study used Maximum Entropy to determine current and future distributions of *Hypericum pseudohenryi* in South Africa. Under current climatic conditions using data from the invaded range, the model identifies climatically suitable habitat for *Hypericum pseudohenryi* extending across the eastern parts of the KwaZulu-Natal Drakensberg, high altitude areas of the Eastern Cape, Mpumulanga and Limpopo provinces (Fig 4.1). Average model accuracy over the 30 runs was high (AUC = 0.993). The maps only show areas where there is a 50% or greater chance of *H. pseudohenryi* occurring (Fig 4.1). The results show that *H. pseuodhenryi* has the potential to occupy an area of 298.1 km^2 in South Africa. While populations have been previously found in KwaZulu-Natal and the Eastern Cape, there were no known populations of *H. pseudohenryi* in Mpumulanga and Limpopo provinces at the beginning of this study, thus suggesting that *H. pseudohenryi* is suited to areas beyond the current distribution in South Africa.

Data from the native range in China showed differences in the climate niche of *H. pseudohenryi* in South Africa (Fig 4.2). Most notably is the lack of climatically suitable areas occurring in the Eastern Cape in the prediction. Climatically suitable habitats extend west of the Drakensberg mountain range as well as east towards the KwaZulu-Natal Midlands.

4.3.2 Future distribution: scenario RCP 2.6

Under scenario RCP 2.6, where greenhouse gas emissions are currently peaking and global temperatures are expected to increase by 1°C by 2070, there is a range contraction of *H. pseudohenryi* throughout South Africa (Fig 4.3). The area that is climatically suitable for *H. pseudohenryi* decreases by 63.3% by 2050, however, by 2070 the area that is climatically suitable for *H. pseudohenryi* in South Africa increases by 17.3% from 2050 (Fig 4.4). Model accuracy for both future condition models were excellent (2050 AUC = 0.995; 2070 AUC = 0.996). The predicted range of *H. pseudohenryi* decreases in Mpumulanga and the area in Limpopo Province becomes climatically unsuitable under scenario RCP 2.6.

4.3.3 Future distribution: scenario RCP 6.0

Under scenario RCP 6.0, where greenhouse gas emissions will peak in 2080 and global temperatures are expected to increase by 2.2°C by 2070, the range contraction is less pronounced compared to RCP 2.6 (Fig 4.3). The potential area occupied by *H. pseudohenryi* decreases by 46.2% by 2050 and 51.2% by 2070 (Fig 4.4). Model accuracy was excellent for both the future condition models (2050 and 2070 AUC = 0.995). As in scenario RCP 2.6, the northern region is expected to become climatically unsuitable under future conditions, however, there is an increase in climatically suitable areas in the Drakensberg range, especially into Lesotho. Scenario RCP 6.0 shows a decrease in the range of climatically suitable area in the Eastern Cape region.

4.4. Discussion

4.4.1 Climate niche under current climatic conditions

The results of this study indicate that *Hypericum pseudohenryi* has yet to realise the full extent of climatically suitable habitat in South Africa under current climatic conditions. Plant species that have had a relatively short residence time in a country often have not yet had time to expand their range throughout the full extent of the environment, which could account for the results of this study (Wilson *et al.*, 2007), however, it is not known when *H. pseudohenryi* was introduced into South Africa. The model suggests that climatically suitable habitat currently occurs across the eastern regions of South Africa, particularly in the KwaZulu-Natal Midlands and Drakensberg mountains (Fig 4.1). Smaller areas that may be suitable for *H. pseudohenryi* are found in Mpumulanga, Limpopo and the Eastern Cape. As seeds may be dispersed via wind or water, the ability to fully realise all climatically suitable habitats may be hindered by seed dispersal (Beaumont *et al.*, 2009a). However, accidental transportation of seeds by humans on shoes or car tyres may drive dispersal to new habitats (Dullinger *et al.*, 2009). The predictive model of the fundamental niche of *H. pseudohenryi* in South Africa helps managers to focus on specific areas for investigating new populations (Kaplan *et al.*, 2014).

Climate niche models predicted different climatic niches from data of the native range compared to data of the invaded range (Fig 4.2). This is consistent with several studies that have shown invasive alien plants undergo climate niche shifts in the invaded range (Broennimann *et al.*, 2007, Beaumont *et al.*, 2009b). The climate niche model using the native range does not indicate climatically suitable habitats occurring in the Eastern Cape, where large populations have been found (Pers. obs.). However, areas in the KwaZulu-Natal Drakensberg and Midlands, Mpumulanga and Limpopo show similar trends in climatically suitable habitat regardless of dataset used.

Comparing the two models, using native range versus the introduced range of *H. pseudohenryi*, data from the introduced range gave a more accurate model than the data from the native range. One of the reasons for the difference in models could be due to the native range having a very small sample size that may not have included all potential populations, while the introduced range was widely sampled. If there is a large database for the introduced range, as there was in this study, it is suggested that introduced range data be used in climate models in order to give the most detailed model for the species in the introduced range.

4.4.2 Climate niche under future climatic conditions

Under future climatic conditions, climate niche models in both scenarios indicate that spread of *H. pseudohenryi* will be hindered with increasing temperatures. Loss of climatically suitable habitat will occur primarily in the northern range of climatically suitable areas (Fig 4.4), which is expected to become hotter and drier under both scenarios (Boko *et al.*, 2007). Under scenario RCP 6.0, loss of climatically suitable habitat is expected in the mountainous regions of the Eastern Cape. The increase in climatically suitable habitats in 2070 under RCP 2.6 may be as a result of stabilisation of the climate under this scenario, with a greater area being climatically suitable compared to conditions in 2050. The increased probability of *H. pseudohenryi* occurring in the Drakensberg region is due to predicted increases in summer rainfall in this region in the future (Hewitson & Crane, 2006). The shift in climatically suitable habitat into pristine regions at higher elevation poses a risk to biodiversity in the Drakensberg region. Studies have found similar results for cold-adapted grasses (Parker-Allie *et al.*, 2009) and herbs (Beaumont *et al.*, 2009a), as high altitudes will provide pockets with temperatures within suitable range for germination of seeds and growth. Shifts in climate niche of *H. pseudohenryi* due to climate change offer unique management opportunities. Areas no longer suitable for *H. pseudohenryi* can be restored with native species that are suited to the new climatic conditions (Bradley & Wilcove, 2009).

4.4.3 Limitations of climate niche modelling

While climate niche modelling is a useful tool for predicting future distribution patterns of invasive alien plant species, there are limitations to the interpretation of results. Choice of climate model and the parameters used in the model are factors that can influence the results of the prediction. In general, several assumptions are made in climate niche modelling: 1) climate is the only factor influencing the species range; 2) biotic interactions do not influence geographic range of a species, and remain constant in space and time; 3) genetic and phenotypic composition of species is constant in space and time; 4) dispersal is not limited and the species occurs over the entire suitable range (Jeschke & Strayer, 2008, Beaumont *et al.*, 2009b). These assumptions do not hold true for species distributions in real habitats and ecosystems. Species range is affected by factors other than climate, such as soil type, level of disturbance and topography (Baret *et al.*, 2006) and these factors may be enhanced or weakened with altered future climates (Beaumont *et al.*, 2009a). A study by Murray *et al.* (2012) found that climatically suitable area decreased when adding the species' interactions with the habitat and species traits to their climate niche model of *Phyla canescens* in the United States. Populations of invasive alien plants that reproduce sexually are not genetically static. Rather, phenotypic variation and genetic diversity can be high in invasive alien populations, especially if there have been multiple introductions from several sources (Lavergne & Molofsky, 2007). Species occurrence is not only a function of environmental conditions but also neighbouring populations, indicating that propagule pressure is a significant driver of colonisation (Thomas & Moloney, 2013). Several studies have suggested that to increase accuracy of climate niche models factors such as proxies for propagule pressure and use of ecophysiological traits need to be included in the model (Tsoar *et al.*, 2007, Beaumont *et al.*, 2009a, Dullinger *et al.*, 2009, Fennell *et al.*, 2012).

Sample size and record accuracy across the species' current range are important for accurate predictive models. When a small set of localities are used in climate niche models, there is not enough representative data of a species climatic tolerances (Welk, 2004). Errors occur when few scattered locations throughout the region are used, resulting in an overestimation of climatically suitable areas (Rouget *et al.*, 2004). Similarly, underestimation arises from species occurring in small clumped areas across the region (Rouget *et al.*, 2004). Use of distributional data from the native range can create more accurate predictions due to larger sample sizes (Welk, 2004), however if there has been a climate niche shift in the naturalised range, predictions will still be inaccurate (Broennimann *et al.*, 2007). Spatial scale is important depending on the problem being explored with the predictive model (Murray *et al.*, 2012). Large spatial scales can be used as a general indicator for identifying areas globally that may have climatically similar habitats as a species prior to exportation (Richardson & Thuiller, 2007), while smaller spatial scales are better for determining local effects of IAPs (Murray *et al.*, 2012).

Climatic niche modelling predicts the full range of climatically suitable areas where the species is able to survive, known as the fundamental niche of the species. However, not all areas become colonised, resulting in the realised niche, where the species is actually found (Jiménez-Valverde *et al.*, 2011). Factors such as dispersal, competitive abilities and competition from native species affect the distribution of invasive alien species in the naturalised range (Beaumont *et al.*, 2009a). These factors, while important in species' distributions, are often not included in climate niche models (Tsoar *et al.*, 2007). One approach that can create better predictive models is the use of hierarchies, as this method includes factors such as land use, land cover, dispersal vectors and plant functional traits (Thomas & Moloney, 2013). Mechanistic models simulate dynamic factors affecting the spread of a species throughout an environment, creating models that closely reflect the realised niche of the invasive alien species (Fennell *et al.*, 2012).

Clearing of invasive alien plants can also have an effect on climate niche model predictions. Climate niche models do not take into account clearing efforts as removal of plants results in a decrease of propagules from the system. Cleared populations need to be recorded as a lack of these records can result in lowered accuracy of predictive models (Higgins *et al.*, 1999). One of the factors that many management plans neglect is the increased likelihood that clearing one species is likely to result in replacement by another invasive alien species (Foxcroft *et al.*, 2007). Climate niche modelling can be used to determine which species could threaten newly cleared areas for monitoring as regrowth occurs.

4.5. Conclusions

Naturalised populations of *Hypericum pseudohenryi* have not yet realised all climatically suitable areas in South Africa under current climatic conditions. Use of native range data results in areas where known populations occur not being identified in South Africa. In the future, as climate change progresses, there will be a reduction in climatically suitable habitat; however, there will be increased probabilities of *H. pseudohenryi* occurring at high altitude areas in the Drakensberg. The presence of dense stands of *H. pseudohenryi* in the Drakensberg region will negatively affect species endemic to this region. Management of *H. pseudohenryi* in South Africa needs to focus efforts on clearing in the higher altitude areas of the Drakensberg region while populations are still at manageable sizes and densities. While the costs of clearing at high altitudes are expensive due the need for specialised teams, the risk of species loss needs to be weighed against the financial implications.

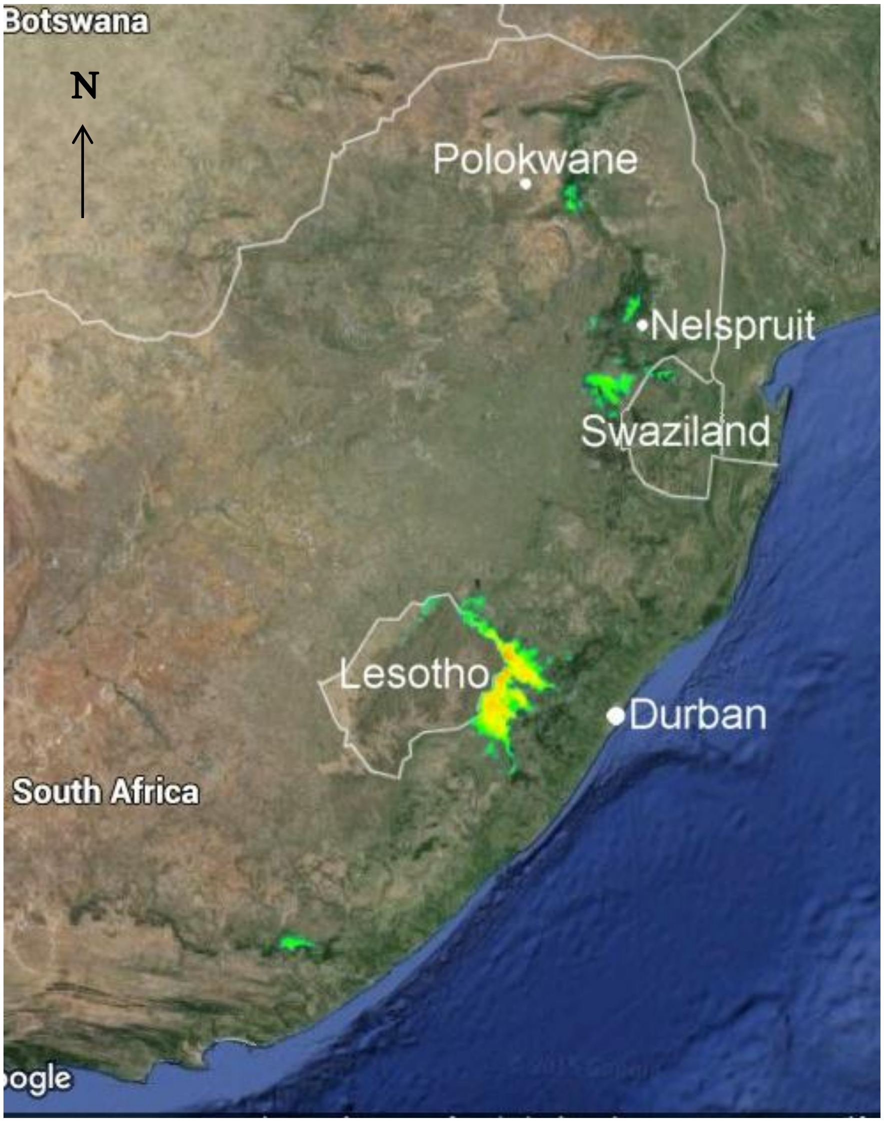

Fig. 4.1: The predicted climate niche of *Hypericum pseudohenryi* under current climatic conditions using data from the invaded range. Green represents areas with a 50% probability of climatically suitable habitat, and red represents areas of 100% probability of climatically suitable habitat.

Fig. 4.2: The predicted climate niche of *Hypericum pseudohenryi* under current climatic conditions using data from the native Chinese range. Green represents areas with a 50% probability of climatically suitable habitat, and red represents areas of 100% probability of climatically suitable habitat.

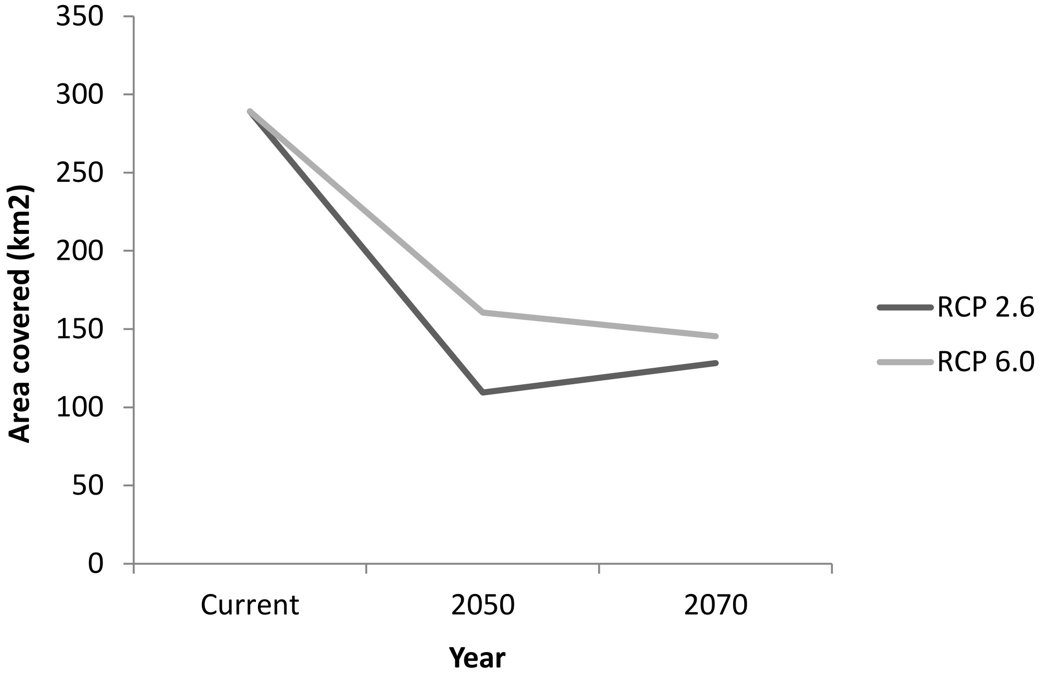

Fig. 4.3: Change in area (km^2) that is climatically suitable for *H. pseudohenryi* in South Africa under current and future (2050 and 2070) conditions for the scenarios RCP 2.6 and RCP 6.0.

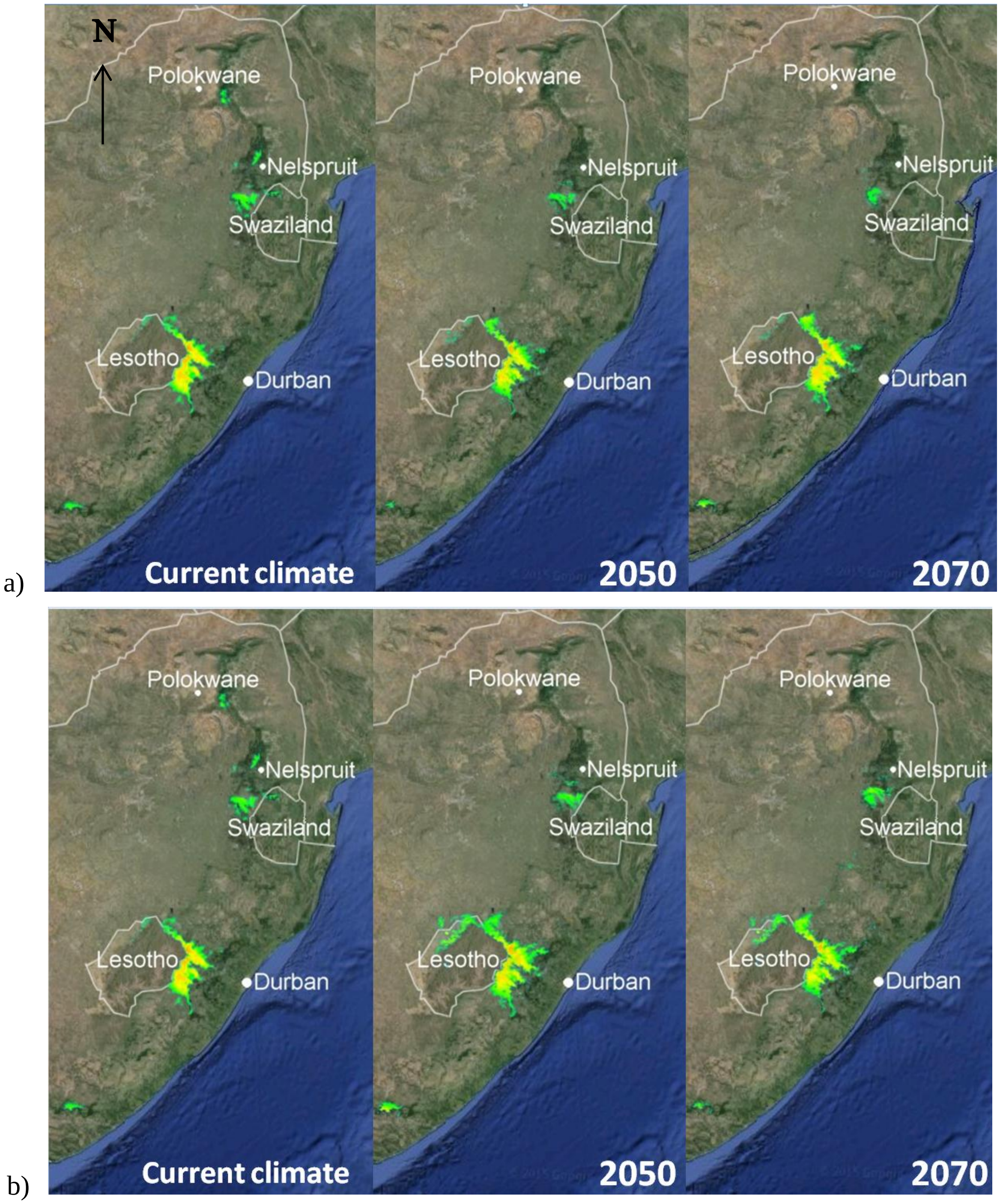

Fig. 4.4: Comparison of current and future climatically suitable regions in South Africa under a) scenario RCP 2.6 and b) scenario 6.0 for the years 2050 and 2070. Green represents areas with a 50% probability of climatically suitable habitat, and red represents areas of 100% probability of climatically suitable habitat.

Chapter 5

Conclusions

One of the major threats to biodiversity in South Africa are invasive alien plants. Emerging invasive alien species, such as *Hypericum pseudohenryi* has the potential to be eradicated through proper management of the species in the invaded range. As very little information about *H. pseudohenryi* was available, both in the native range and in the invaded range in South Africa, the work done in this study was to help improve the knowledge base in order to make good management decisions.

A review of the literature of invasive alien plants in South Africa shows a bias towards studies of invasive alien plants in the Western Cape region, primarily of the fynbos biome, and to studies of invasive alien tree species. The impacts of invasive alien plants in South Africa are mainly due to habitat transformation, as IAPs alter the structure of the vegetation, leading to changes in ecosystem processes. Dense infestations result in changes to nutrient cycling, hydrological processes and fire regimes. One of the reasons these dense stands occur is because of prolific seed output by IAPs, and the seedlings having adaptations allowing them to outcompete the natural vegetation. Management of IAPs in South Africa has had success, especially through biological control methods. The Working for Water programme has helped reduce water loss from invasive trees, but there is debate as to whether it has been useful in combating the spread of invasive alien plants.

The study of the breeding system revealed that *H. pseudohenryi* is self-compatible and able to produce a small number of seeds through autogamous self-fertilisation. This is an important finding, as it helps to understand the risk of spread from single propagules. Despite the ability to set seed through autogamous self-fertilisation, *H. pseudohenryi* is partially pollinator dependant, with greatest number of seeds being set in hand self-pollinated flowers. Seeds resulting from cross-pollination had slightly higher germination rates, which could indicate inbreeding depression in the populations studied.

In order to understand the full extent of climatically suitable habitats available in South Africa for *H. pseudohenryi*, climate niche modelling was employed. The model showed that *H. pseudohenryi* has not yet realised its full climatic niche in South Africa, and that areas in

Mpumulanga and Limpopo could be invaded by *H. pseudohenryi* if measures are not taken to prevent introduction of the species into these areas. In the future, under climate change, the amount of climatically suitable habitat in South Africa decreases, however under both climate change scenarios, the high altitude areas of the KwaZulu-Natal Drakensberg remain climatically suitable for *H. pseudohenryi*.

In an ideal world, removal of *H. pseudohenryi* plants should occur across the currently invaded range. However, as budgets limit management options, certain areas of invasion should be prioritised. Monitoring activities should be conducted regularly in Mpumulanga and Limpopo provinces, where the invasion has not yet occurred. Should populations be found in these regions, removal should occur as soon as possible in order to contain the spread before the plant becomes widespread. The cost of removal operations early in the invasion process is also more cost effective. In areas currently invaded, priority should be given to the Drakensberg region, where plants have become a problem along streams and on dry slopes. As the probability for climatically suitable habitat occurring in high altitude areas in the Drakensberg in the future, these areas should be the main focus for removal efforts. Areas that have been cleared must be monitored for growth of seedlings for a few years after clearing efforts to prevent infestations from occurring again. During removal, care should be taken to prevent the spread of seeds back into the environment, and thus removal should occur before March, when seed pods begin to dehisce.

As there has been little information available for *H. pseudohenryi*, the species has not yet been categorised under the NEM:BA regulations. As the populations are only located in KwaZulu-Natal and the Eastern Cape, eradication of the species is possible. It is thus recommended that *H. pseudohenryi* be categorised as a Category 1a species in the NEM:BA regulations. This will help to give priority to eradication efforts in South Africa.

Further work on *H. pseudohenryi* could focus on eradication of the species. Currently, eradication efforts involve applying herbicide to cut stumps. Determining the best herbicide treatment and concentration will help make eradication efforts more cost effective, which will result in a greater number of plants being removed each summer season. Other studies could focus on how *H. pseudohenryi* is able to spread across the landscape. It is thought that seeds are carried downstream in water courses, however, plants have been found high upstream from main infestations, which suggests that there may be another driver of spread.

Studies of emerging invasive alien plants are important to help prevent further spread through the environment and to contain the species prior to it becoming widespread. Research in South Africa should broaden the scope from studies focused on the fynbos and on invasive alien trees. Management of species other than trees need to be investigated and implemented if the spread of invasive alien species is to be effectively controlled. The grassland biome was identified as the second worst invaded biome after the fynbos, and should be the subject of further research initiatives. The research derived from this study highlights the vast diversity of research that can be done on invasive alien plants in South Africa.

References

Baker, H. G. 1955. Self-compatibility and establishment after 'long-distance' dispersal. Evolution 9, 347-349.

Baker, H. G. 1967. Support for Baker's Law - As a rule. Evolution 21, 853-856.

Baret, S., Rouget, M., Richardson, D. M., Lavergne, C., Egoh, B., Dupont, J., Strasberg, D. 2006. Current distribution and potential extent of the most invasive alien plant species on La Réunion (Indian Ocean, Mascarene islands). Austral Ecology 31, 747-758.

Beaumont, L. J., Gallagher, R. V., Downey, P. O., Thuiller, W., Leishman, M. R., Hughes, L. 2009a. Modelling the impact of *Hieracium* spp. on protected areas in Austrailia under future climates. Ecography 32, 757-764.

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

Bird, M. S., Day, J. A. 2014. Wetlands in changed landscapes: The influence of habitat transformation on the physico-chemistry of temporary depression wetlands. PLoS ONE 9, e88935.

Bird, M. S., Day, J. A., Rebelo, A. J. 2013. Physico-chemical impacts of terrestrial alien vegetation on temporary wetlands in a sclerophyllous Sand fynbos ecosystem. Hydrobiologia 711, 115-128.

Blackburn, T. M., Pysek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarosik, V., Wilson, J. R. U., Richardson, D. M. 2011. A proposed unified framework for biological invasions. Trends in Ecology & Evolution 23, 333-339.

Blanchard, R., Holmes, P. M. 2008. Riparian vegetation recovery after invasive alien tree clearance in the Fynbos Biome. South African Journal of Botany 74, 421-431.

Blumenthal, D., Mitchell, C. E., Pyšek, P., Jarošík, V. 2009. Synergy between pathogen release and resource availability in plant invasion. Proceedings of the National Academy of Science 106, 7899-7904.

Boko, M., Niang, I., Nyong, A., Vogel, C., Githeko, A., Medany, R., Osman-Elasha, B., Tabo, R., Yanda, P. 2007. Africa. Climate Change 2007: Impacts, Adaptation and Vulnerability. In M. L. Parry, O. F. Canziani, J. P. Palutikof, v. d. L. P.J., C. E. Hanson, eds. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Bradley, B. A., Wilcove, D. S. 2009. When invasive plants disappear: Transformative restoration possibilities in the western United States resulting from climate change. Restoration Ecology 17, 715-721.

Bradley, B. A., Wilcove, D. S., Oppenheimer, M. 2010. Climate change increases risk of plant invasion in the Eastern United States. Biological Invasions 12, 1855-1872.

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

Bromilow, C. 2010. Problem Plants and Alien Weeds of South Africa. 3rd edition. Briza Publications, Pretoria.

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., Hobbs, R. J., Pellant, M., Pyke, D. 2004. Effects of invasive alien plants on fire regimes. BioScience 54, 677-688.

Brown, J. R., Bestelmeyer, B. T. 2012. Managing Invasive Species in Heterogenous Ecosystems. In T. A. Monaco, R. L. Sheley, eds. Invasive Plant Ecology and Management: Linking Processes to Practice. CABI, Oxfordshire.

Burke, M. J. W., Grime, J. P. 1996. An Experimental Study of Plant Community Invasibility. Ecology 77, 776-790.

Burns, J. H., Ashman, T.-L., Steets, J. A., Harmon-Threatt, A., Knight, T. M. 2011. A phylogenetically controlled analysis of the roles of reproductive traits in plant invasions. Oecologia 166, 1009-1017.

Busch, J. W., Delph, L. F. 2012. The relative importance of reproductive assurance and automatic selection as hypotheses for the evolution of self-fertilization. Annals of Botany 109, 553-562.

Callaway, R. M., Ridenour, W. M. 2004. Novel weapons: Invasion sucess and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2, 436-443.

Carbutt, C. 2012. The emerging invasive alien plants of the Drakensberg Alpine Centre, southern Africa. Bothalia 42, 71-85.

Castro-Díez, P., Langendoen, P., Poorter, P., Saldanã-López, P. 2011. Predicting *Acacia* invasive success in South Africa on the basis of functional traits, native climatic niche and human use. Biodiversity Conservation 20, 2729-2743.

Charlesworth, D., Charlesworth, B. 1987. Inbreeding depression and its evolutionary consequences. Annual review of Ecology and Systematics 18, 237-268.

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

Colautti, R. I., MacIssac, H. J. 2004. A neutral terminology to define 'invasive' species. Diversity and Distributions 10, 135-141.

Cousens, R., Mortimer, M. 1995. Dynamics of Weed Populations. Cambridge University Press, Cambridge.

Crockett, S. L., Robson, N. K. B. 2011. Taxonomy and Chemotaxonomy of the genus *Hypericum*. Medicinal and Aromatic Plant Science and Biotechnology 5, 1-13.

Cronk, Q. C. B., Fuller, J. L. 2001. Plant Invaders: The Threat to Natural Ecosystem. Earthscan, New York.

Crous, C. J., Jacobs, S. M., Esler, K. J. 2012. Drought-tolerance of an invasive alien tree, *Acacia mearnsii* and two native competitors in fynbos riparian ecotones. Biological Invasions 14, 619-631.

Cullis, J. D. S., Görgens, A. H. M., Marais, C. 2007. A strategic study of the impact of invasive alien plants in the high rainfall catchments and riparian zones of South Africa on total surface water yield. Water SA 33, 35-42.

Davis, M. A., Grime, J. P., Thompson, K. 2000. Fluctuating resources in plant communities: A general theory of invasibility. Journal of Ecology 88, 528-534.

de Neergaard, A., Saarnak, C., Hill, T., Khanyile, M., Berzosa, A. M., Birch-Thomsen, T. 2005. Australian wattle species in the Drakensberg region of South Africa – An invasive alien or a natural resource? Agriculture Systems 85, 216-233.

Donaldson, J. E., Richardson, D. M., Wilson, J. R. U. 2014. The seed ecology of an ornamental wattle in South Africa — Why has *Acacia elata* not invaded a greater area? South African Journal of Botany 94, 40-45.

Drenovsky, R. E., Grewell, B. J., D'Antonio, C. M., Funk, J. L., James, J. J., Molinari, N., Parker, I. M., Richards, C. L. 2012. A functional trait perspective on plant invasion. Annals of Botany 110, 141-153.

Dukes, J. S., Mooney, H. A. 1999. Does global change increase the sucess of biological invaders? Trends in Ecology and Evolution 14, 135-139.

Dullinger, S., Kleinbauer, I., Peterseil, J., Smolik, M., Essl, F. 2009. Niche based distribution modelling of an invasive alien plant: Effects of population status, propagule pressure and invasion history. Biological Invasions 11, 2401-2414.

DWAF (D. o. W. A. a. Forestry). National Water Resource Strategy. Department of Water Affairs and Forestry, Pretoria.

Dye, P., Jarmain, C. 2004. Water use by black wattle (*Acacia mearnsii*): Implications for the link between removal of invading trees and catchment streamflow response. South African Journal of Science 100, 40-44.

Dzikiti, S., Schachtschneider, K., Naiken, V., Gush, M., Moses, G., Le Maitre, D. C. 2013. Water relations and the effects of clearing invasive *Prosopis* trees on groundwater in an arid environment in the Northern Cape, South Africa. Journal of Arid Environments 90, 103-113.

Eckert, C. G., Kalisz, S., Geber, M. A., Sargent, R., Elle, E., Cheptou, P.-O., Goodwillie, C., Johnston, M. O., Kelly, J. K., Moeller, D. A., Porcher, E., Ree, R. H., Vallejo-Marin, M., Winn, A. A. 2009. Plant mating systems in a changing world. Trends in Ecology and Evolution 25, 35-43.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6, 503-523.

Fennell, M., Murphy, J. E., Armstrong, C., Gallagher, T., Osborne, B. 2012. Plant spread simulator: A model for simulating large-scale directed dispersal processes across heterogeneous environments. Ecological Modelling 230, 1-10.

Foxcroft, L. C., Rouget, M., Richardson, D. M. 2007. Risk assessment of riparian plant invasions into protected areas. Conservation Biology 21, 412-421.

Fuhlendorf, S. D., Allred, B. W., Elmore, D., Engle, D. M. 2012. Linking disturbance regimes, vegetation dynamics and plant strategies across complex landscapes to mitigate and manage plant invasions. In T. A. Monaco, R. L. Sheley, eds. Invasive Plant Ecology and Management: Linking Processes to Practice. CABI, Oxfordshire.

Geerts, S., Botha, P. W., Visser, V., Richardson, D. W., Wilson, J. R. U. 2013a. Montpellier broom (*Genista monspessulana*) and Spanish broom (*Spartium junceum*) in South Africa: An assessment of invasiveness and options for management. South African Journal of Botany 87, 134-145.

Geerts, S., Moodley, D., Gaertner, M., Le Roux, J. J., Mcgeoch, M. A., Muofhe, C., Richardson, D. M., Wilson, J. R. U. 2013b. The absence of fire can cause a lag phase: The invasion dynamics of *Banksia ericifolia* (Proteaceae). Austral Ecology 38, 931-941.

Gerber, E., Krebs, C., Murrell, C., Moretti, M., Rocklin, R., Schaffner, U. 2008. Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. Biological Conservation 141, 646-654.

Görgens, A. H. M., Van Wilgen, B. W. 2004. Invasive alien plants and water resources in South Africa: Current understanding, predictive ability and research challenges. South African Journal of Science 100, 27-33.

Grant, T. A., Paschke, M. W. 2012. Invasive plant impacts on soil properties, nutrient cycling and microbial communities. In T. A. Monaco, R. L. Sheley, eds. Invasive Plant Ecology and Management: Linking Processes to Practice. CABI, Oxfordshire.

Harmon-Threatt, A., Burns, J. H., Shemyakina, L. A., Knight, T. M. 2009. Breeding system and pollination ecology of introduced plants compared to their native relatives. American Journal of Botany 96, 1544-1550.

Henderson, L. 2006. Comparisons of invasive plants in southern Africa originating from southern temperate, northern temperate and tropical regions. Bothalia 36, 201-222.

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

Hewitson, B. C., Crane, R. G. 2006. Consensus between GCM climate change projections with empirical downscaling: precipitation downscaling over South Africa. International Journal of Climatology 26, 1315-1337.

Hierro, J. L., Maron, J. L., Callaway, R. M. 2005. A biogeographical approach to plant invasion: The importance of studying exotics in their introduced and native range. Journal of Ecology 93, 5-15.

Higgins, S. I., Richardson, D. M., Cowling, R. M., Trinder-Smith, T. H. 1999. Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. Conservation Biology 13, 303-313.

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

Hugo, S., van Rensburg, B. J., van Wyk, A. E., Steenkamp, Y. 2012. Alien phytogeographic regions of southern Africa: Numerical classification, possible drivers, and regional threats. PLoS ONE 7, e36269.

Iponga, D. M., Milton, S. J., Richardson, D. M. 2009a. Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Anacardiaceae) in South Africa. Austral Ecology 34, 678-687.

Iponga, D. M., Milton, S. J., Richardson, D. M. 2009b. Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna. Biological Invasions 11, 159-169.

Jacobs, L. E. O., Richardson, D. M., Wilson, J. R. U. 2014. *Melaleuca parvistaminea* Byrnes (Myrtaceae) in South Africa: Invasion risk and feasibility of eradication. South African Journal of Botany 94, 24-32.

Jeschke, J. M., Strayer, D. L. 2008. Usefulness of bioclimatic models for studying climate change and invasive species. Annals of the New York Academy of Sciences 1134, 1-24.

Jiménez-Valverde, A., Peterson, A. T., Soberón, J., Overton, J. M., Aragón, P., Lobo, J. M. 2011. Use of niche models in invasive species risk assessments. Biological Invasions 13, 2785-2797.

Jordaan, L. A., Downs, C. T. 2012. Comparison of germination rates and fruit traits of indigenous *Solanum giganteum* and invasive *Solanum mauritianum* in South Africa. South African Journal of Botany 80, 13-20.

Kalwij, J. M., Robertson, M. P., van Rensburg, B. J. 2008. Human activity facilitates altitudinal expansion of exotic plants along a road in montane grassland, South Africa. Applied Vegetation Science 11, 491-498.

Kalwij, J. M., Steyn, C., le Roux, P. C. 2014. Repeated monitoring as an effective early detection means: first records of naturalised *Solidago gigantea* Aiton (Asteraceae) in southern Africa. South African Journal of Botany 93, 204-206.

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

Keane, R. M., Crawley, M. J. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17, 164-170.

Keeley, J. E. 2001. Fire and invasive species in Mediterranean-climate ecosystems of California.*in* K. E. M. Galley, T. P. Wilson, editors. First National Congress on Fire Ecology, Prevenrion, and Manageement. Miscellaneous Publication, Tall Timbers Research Station.

Kohli, R. K., Dogra, K. S., Batish, D. R., Singh, H. P. 2004. Impact of invasive plants on the structure and composition of natural vegetation of Northwestern Inandian Himalayas. Weed Technology 18, 1296-1300.

Krug, R. M., Roura-Pascual, N., Richardson, D. M. 2010. Clearing of invasive alien plants under different budget scenarios: Using a simulation model to test efficiency. Biological Invasions 12, 4099-4112.

Lavergne, S., Molofsky, J. 2007. Increased genetic variation and evolutionary potential drive the sucess of an invasive grass. Proceedings of the National Academy of Science 104, 3883-3888.

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

Le Maitre, D. C., Kotzee, I. M., O’Farrell, P. J. 2014. Impacts of land-cover change on the water flow regulation ecosystem service: Invasive alien plants, fire and their policy implications. Land Use Policy 36, 171-181.

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

Leffler, A. J., Ryel, R. J. 2012. Resource pool dynamics. Pages 57-78. In T. A. Monaco, R. L. Sheley, eds. Invasive plant management: linking processes to practice. CABI, Wallingford.

Levin, D. A. 2010. Environment-enhanced self-fertilization: implications for niche shifts in adjacent populations. Journal of Ecology 98, 1276–1283.

Lloret, F., Médail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambdon, P., Hulme, P. E. 2005. Species attributes and invasion success by alien plants on Mediterranean islands. Journal of Ecology 93, 512-520.

MacDonald, I. A. W. 2004. Recent research on alien plant invasions and their management in South Africa: A review of the inaugural research symposium of the Working for Water programme. South African Journal of Science 100, 21-26.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., Bazzaz, F. A. 2000. Biotic invasions: Causes, epidemology, global consequences and control. Ecological Applications 10, 689-710.

Marais, C., Wannenburgh, A. M. 2008. Restoration of water resources (natural capital) through the clearing of invasive alien plants from riparian areas in South Africa — Costs and water benefits. South African Journal of Botany 74, 526-537.

Matzk, F., Hammer, K., Schubert, I. 2003. Coevolution of apomixis and genome size within the genus *Hypericum*. Sexual Plant Reproduction 16, 51-58.

McConnachie, M. M., Cowling, R. M., van Wilgen, B. W., McConnachie, D. A. 2012. Evaluating the cost-effectiveness of invasive alien plant clearing: A case study from South Africa. Biological Conservation 155, 128-135.

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

Milton, S. J. 2004. Grasses as invasive alien plants in South Africa. South African Journal of Science 100, 69-75.

Mokotjomela, T. M., Hoffmann, J. H., Downs, C. T. 2015. The potential for birds to disperse the seeds of *Acacia cyclops*, an invasive alien plant in South Africa. Ibis 157, 449-458.

Moodley, D., Geerts, S., Rebelo, T., Richardson, D. M., Wilson, J. R. U. 2014. Site-specific conditions influence plant naturalization: The case of alien Proteaceae in South Africa. Acta Oecologica 59, 62-71.

Morgan, M. T., Wilson, W. G., Knight, T. M. 2005. Plant population dynamics, pollinator foraging, and the selection of self-fertilization. The American Naturalist 166, 169-183.

Morris, T. L., Barger, N. N., Cramer, M. D. 2015. Competitive resistance of a native shrubland to invasion by the alien invasive tree species, *Acacia cyclops*. Biological Invasions 17, 3563-3577.

Murray, J. V., Stokes, K. E., van Klinken, R. D. 2012. Predicting the potential distribution of a riparian invasive plant: The effects of a changing climate, flood regimes and land-use patterns. Global Change Biology 18, 1738-1753.

Murren, C. J., Dudash, M. R. 2012. Variation in inbreeding depression and plasticity across native and non-native field environments. Annals of Botany 109, 621-632.

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

Parker-Allie, F., Musil, C. F., Thuiller, W. 2009. Effects of climate warming on the distributions of invasive Eurasian annual grasses: A South African perspective. Climatic Change 94, 87-103.

Pejchar, L., Mooney, H. A. 2009. Invasive species, ecosystem services and human well-being. Trends in Ecology and Evolution 24, 497-504.

Petanidou, T., Godfree, R. C., Song, D. S., Kantsa, A., Dupont, Y. L., Waser, N. M. 2012. Self-compatibility and plant invasiveness: Comparing species in native and invasive ranges. Perspectives in Plant Ecology, Evolution and Systematics 14, 3-12.

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

Phillips, S. J., Anderson, R. P., Schapire, R. E. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231-259.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., Tsomondo, T. 2001. Economic and environmental threats of alien plant, animal and microbe invasions. Agriculture, ecosystems & environment 84, 1-20.

Potgieter, L. J., Richardson, D. M., Wilson, J. R. U. 2014. *Casuarina cunninghamiana* in the Western Cape, South Africa: Determinants of naturalisation and invasion, and options for management. South African Journal of Botany 92, 134-146.

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

Pujol, B., Zhou, S.-R., Sanchez Vilas, J., Pannell, J. R. 2009. Reduced inbreeding depression after species range expansion. Proceedings of the National Academy of Science 106, 15379-15383.

Pyšek, P. 1995. On the terminology used in plant invasion studies. Pages 71-81. In P. Pyšek, K. Prach, M. Rejmánek, M. Wade, eds. Plant invasions: general aspects and special problems. Academic Publishing, Amsterdam.

Rahlao, S. J., Milton, S. J., Esler, K. J., Barnard, P. 2014. Performance of invasive alien fountain grass (*Pennisetum setaceum*) along a climatic gradient through three South African biomes. South African Journal of Botany 91, 43-48.

Rambuda, T. D., Johnson, S. D. 2004. Breeding systems of invasive alien plants in South Africa: Does Baker's rule apply? Diversity and Distributions 10, 409-416.

Reinhardt, C. 2012. Alien invader plants in South Africa: Management and challenges.*in* International Symposium: Current Trends in Plant Protection UDK.

Rejmánek, M. 1996. A theory of seed plant invasiveness: The first sketch. Biological Conservation 78, 171-181.

Rejmánek, M., Richardson, D. M. 1996. What attributes make some plants more invasive? Ecology 77, 1655-1661.

Richardson, D. M., Holmes, P. M., Esler, K. J., Galatowitsch, S. M., Stromberg, J. C., Kirkman, S. P., Pysek, P., Hobbs, R. J. 2007. Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Diversity and Distributions 13, 126-139.

Richardson, D. M., Iponga, D. M., Roura-Pascual, N., Krug, R. M., Milton, S. J., Hughes, G. O., Thuiller, W. 2010. Accommodating scenarios of climate change and management in modelling the distribution of the invasive tree *Schinus molle* in South Africa. Ecography 33, 1049-1061.

Richardson, D. M., Pyšek, P., Carlton, J. T. 2011. A compendium of essential concepts and terminology in invasion ecology. In D. M. Richardson, ed. Fifty Years of Invasion Ecology: The legacy of Charles Elton. John Wiley & Sons.

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

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

Richardson, D. M., Rouget, M., Ralston, S. J., Cowling, R. M., van Rensburg, B. J., Thuiller, W. 2005. Species richness of alien plants in South Africa: Environmental correlates and the relationship with indigenous plant species richness. Ecoscience 12, 391-402.

Richardson, D. M., Thuiller, W. 2007. Home away from home - objective mapping of high-risk source areas for plant introductions. Diversity and Distributions 13, 299-312.

Richardson, D. M., van Wilgen, B. W. 2004. Invasive alien plants in South Africa: How well do we understand the ecological impacts? South African Journal of Science 100, 45-52.

Robson, N. K. B. 1985. Studies in the genus Hypericum L. (Guttiferae): 3. Sections: 1. Campylosporus to: 6a. Umbraculoides. Bulletin of the British Museum (Natural History). Botany., London.

Rodger, J. G., van Kleunen, M., Johnson, S. D. 2013. Pollinators, mates and Allee effects: the importance of self-pollination for fecundity in an invasive lily. Functional Ecology 27, 1023-1033.

Ronce, O., Shaw, F. H., Rousset, F., Shaw, R. G. 2009. Is Inbreeding Depression Lower in Maladapted Populations? A Quantitative Genetics Model. Evolution 63, 1807-1819.

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

Roura-Pascual, N., Richardson, D. M., Chapman, R. A., Hichert, T., Krug, R. M. 2011. Managing biological invasions: charting courses to desirable futures in the Cape Floristic Region. Regional Environmental Change 11, 311-320.

Ruwanza, S., Gaertner, M., Esler, K. J., Richardson, D. M. 2013. Both complete clearing and thinning of invasive trees lead to short-term recovery of native riparian vegetation in the Western Cape, South Africa. Applied Vegetation Science 16, 193-204.

Samways, M. J., Taylor, S. 2004. Impacts of invasive alien plants on Red-Listed South African drgonflies (Odonata). South African Journal of Science 100, 78-80.

Semenya, S., Potgieter, M., Tshisikhawe, M., Shava, S., Maroyi, A. 2012. Medicinal utilization of exotic plants by Bapedi traditional healers to treat human ailments in Limpopo province, South Africa. Journal of Ethnopharmacology 144, 646-655.

Sharma, G. P., Esler, K. J. 2008. Phenotypic plasticity among *Echium plantagineum* populations in different habitats of Western Cape, South Africa. South African Journal of Botany 74, 746-749.

Thabethe, V., Wilson, A.-L., Hart, L. A., Downs, C. T. 2015. Ingestion by an invasive parakeet species reduces germination success of invasive alien plants relative to ingestion by indigenous turaco species in South Africa. Biological Invasions 17, 3029 - 3039.

Thomas, S. M., Moloney, K. A. 2013. Hierarchical factors impacting the distribution of an invasive species: Landscape context and propagule pressure. Landscape Ecology 28, 81-93.

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

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78, 81-92.

Tsoar, A., Allouche, O., Steinitz, O., Rotem, D., Kadmon, R. 2007. A comparative evaluation of presenceonly methods for modelling species distribution. Diversity and Distributions 13, 397-405.

van der Waal, B. W., Rowntree, K. M., Radloff, S. E. 2012. The effect of *Acacia mearnsii* invasion and clearing on soil loss in the Kouga Mountains, Eastern Cape, South Africa. Land Degredation and Development 23, 577-585.

van Gils, H., Mwanangi, M., Rugege, D. 2006. Invasion of an alien shrub across four land management regimes, west of St Lucia, South Africa. South African Journal of Science 102, 9-12.

van Kleunen, M., Fischer, M., Johnson, S. D. 2007. Reproductive assurance through self-fertilization does not vary with population size in the alien invasive plant *Datura stramonium*. Oikos 116, 1400-1412.

van Kleunen, M., Johnson, S. D. 2005. Testing for ecological and genetic Allee effects in the invasive shrub *Senna didymobotrya* (Fabaceae). American Journal of Botany 92, 1124-1130.

van Kleunen, M., Johnson, S. D. 2007. Effects of self-compatibility on the distribution range of invasive European plants in North America. Conservation Biology 21, 1537-1544.

van Wilgen, B. W. 2012. Evidence, perceptions, and trade-offs associated with invasive alien plant control in the Table Mountain National Park, South Africa. Ecology and Society 17, 23.

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

van Wilgen, B. W., Reyers, B., Le Maitre, D. C., Richardson, D. M., Schonegevel, L. 2008. A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. Journal of Environmental Management 89, 336-349.

van Wilgen, B. W., Richardson, D. M. 1985. The effects of alien shrub invasions on vegetation structure and fire behaviour in South African Fynbos shrublands: a simulation study. Journal of Applied Ecology 22, 955-966.

van Wilgen, B. W., Richardson, D. M. 2014. Challenges and trade-offs in the management of invasive alien trees. Biological Invasions 16, 721-734.

Welk, E. 2004. Constraints in range predictions of invasive plant species due to non-equilibrium distribution patterns: Purple loosestrife (*Lythrum salicaria*) in North America. Ecological Modelling 179, 551-567.

Whitney, K. D., Gabler, C. A. 2008. Rapid evolution in introduced species, 'invasive traits' and recipient communities: Challenges for predicting invasive potential. Diversity and Distributions 14, 569-580.

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

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

Zimmermann, H. G., Moran, V. C., Hoffmann, J. H. 2004. Biological control in the management of invasive alien plants in South Africa, and the role of the Working for Water programme. South African Journal of Science 100, 34-40.