PLANT LIFE HISTORY AND THE NATURALISATION TO INVASION PATHWAY

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DECLARATION

This is to certify that:

- (i) The work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.
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……………………………………… Megan L. Phillips

THESIS ABSTRACT

Exotic plant species that become widespread and abundant in their new ranges are a worldwide environmental problem. Such invasive plant species are responsible for a growing number of ecological problems including biodiversity loss, disruptions in ecosystem function and species extinctions. Many exotic plant species introduced to new regions become naturalised, but only a small subset of these species transition from naturalisation to invasion. An important goal of invasion ecology is the identification of plant traits that enable exotic plant species to become invasive within their new ranges. The identification of such traits provides a better understanding of factors contributing to invasion success and contributes to the effective management of invasive plants. In Australia, exotic plant invasion is recognized as a serious and growing threat to native biodiversity. Yet, despite the recognition of the impacts of invasive exotic plant species, there is a paucity of information about the factors contributing to their success in Australia. Thus, identifying plant traits that promote the invasion success of exotic plant species in Australia is a research and management imperative.

This research thesis examined relationships between exotic plant species invasiveness and a range of plant life-history traits through the use of a continental-scale, target-area comparative approach. I compared plant traits between invasive and non-invasive species across multiple plant life-history stages, from seed traits in the seed bank to germination characteristics, seedling emergence and growth traits, as well as the attributes of mature plants. I first constructed a database of 468 naturalised exotic plant species in Australia, with data for four plant introduction traits. I found that residence time (the length of time an exotic plant species has been present in the introduced range) was a consistent predictor of invasion success, as was growth form with the introduction of vines significantly more likely to be linked with invasiveness within Australia. Continental origin was correlated with invasiveness, with invasive species in Australia significantly more likely to originate from North America or South America and less likely to originate from Europe or Australasia. There was no clear indication that exotic species introduced accidentally, as ornamentals or for agricultural purposes were significantly more likely to become invasive.

I then designed a novel species selection framework to closely examine life-history trait differences between invasive and non-invasive naturalised plant species.

Critical to this framework was the need to control for potentially confounding factors that might result in either the emergence of spurious life-history correlates of invasiveness or an inability to find important life-history trait relationships with invasiveness. The species selection framework controlled for the introduction traits residence time, growth form and continental origin, all found to be important correlates of invasiveness in my previous analysis, as well as geographic co-occurrence and range size differences. In the case of the latter two, it was essential to ensure that comparisons between invasive and non-invasive species involved pairs of species that occurred in the same habitats and to ensure that invasive species were substantially more widespread geographically than non-invasive species. Importantly, the framework used information about phylogenetic relationships to provide phylogenetically independent contrasts of life-history traits between invasive and non-invasive species. This species selection framework provided the foundation of all my database and experimental studies in the rest of this thesis.

Using the framework, I conducted an empirical desk-top study to analyse life-history trait relationships with species invasiveness using a complementary cross-species and phylogenetically-independent contrasts approach. The cross-species approach examined trait relationships with invasiveness without explicitly considering the phylogenetic relatedness of the study species. The contrasts approach complemented the cross-species approach by using phylogenetic information to examine patterns of correlated evolutionary divergences between life-history traits and invasiveness. Life-history traits examined in this study included seed mass, leaf size, maximum canopy height, number of dispersal mechanisms and types of dispersal mechanisms used by each species. This study detected two life-history traits linked significantly to invasiveness within the naturalised flora of Australia: an increased number of plant dispersal mechanisms and the use of water as a dispersal mechanism. Both of these traits are intimately connected with a species' capacity to spread across a landscape, which implies enhanced dispersal may be promoting exotic species invasiveness in Australia.

Using a subset of plant species from the desk-top dataset, I performed three separate experiments. In the first experiment, I found evidence on a local scale that the survival of seeds of invasive species in the soil seed bank was significantly higher than seed survival in non-invasive species (in six out of seven congeneric contrasts). I also found that the application of a fungicide treatment led to a larger increase in seed survival in the non-invasive compared with the invasive species, suggesting that poorer seed survival in the non-invasive species could be attributed to seed-deteriorating soil-borne pathogenic fungi present in the new range. In the second experiment, I compared a range of seed germination characteristics between invasive and non-invasive species. I found that the seeds of invasive species germinated significantly more rapidly (in five out of seven contrasts), but were also more likely to exhibit a 'bet-hedging' strategy by staggering seed germination over a longer period of time (in four out of seven contrasts), as well as retaining a higher proportion of dormant but viable seeds after a germination-triggering event occurred (in five out of seven contrasts). In the third experiment, I compared seedling traits between invasive and non-invasive plant species using four congeneric pairs to determine whether there were any consistent trait correlations with species invasiveness. The study explored five seedling traits including time to seedling emergence from the soil, seedling height, leaf production, specific leaf area and biomass. I found evidence that some invasive species differed from non-invasives during the seedling stage, but I found no consistent seedling trait explicitly linked to species invasiveness.

The work presented in this thesis contributes to the quest to identify plant traits facilitating the naturalisation to invasion transition. This thesis used a comparative approach to successfully link exotic plant species invasiveness within the introduced range to plant introduction and life-history traits across a range of plant life stages. The approach and findings of this thesis were built on an important historical and growing body of work examining plant species invasiveness. Given the relative paucity of work specifically focusing on the shift from naturalisation to invasion, this thesis provides information crucial for our understanding and management of the global problem of biological invasions.

ACKNOWLEDGEMENTS

I wish to acknowledge the Australian Research Council for providing the scholarship that funded my PhD and enabled this research to happen. I also wish to thank the School of the Environment, the Faculty of Science and UTS for providing me with a scholarship top-up and support funds for my projects including the many thousands of seeds used in my research. My thanks to the Faculty for providing travel funding that allowed me to present my research findings at the ESA 2010 and ESA 2011 conferences.

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Thank you for everything, my Obi-Wan.

PREFACE

All research presented here was completed for my PhD thesis.

A version of Chapter 2 has been published in the journal *Austral Ecology*.

A version of Chapter 4 has been published in the journal *Evolutionary Ecology Research*.

A version of Chapter 7 has been published in the journal *Preslia*.

Versions of Chapters 3 and 4 have been presented as posters at the Ecological Society of Australia's annual national conference in 2010 and 2011 respectively.

TABLE OF CONTENTS

LIST OF FIGURES AND BOXES

LIST OF TABLES

Chapter 1

General Introduction

1.1 INVASION ECOLOGY AND ITS INCEPTION

Throughout human history, many anecdotes have been made regarding the human-assisted migration of plant and animal species. In 77 AD, the Roman naturalist Gaius Plinius Secundus (also known as Pliny the Elder) published the encyclopaedia '*Historia Naturalis*'. These were among the first scientific texts to describe plagues of mice, moles, and insects across Europe. Pliny reported that the proliferation of rabbits (*Oryctolagus cuniculus*) on the Balearic Islands was so damaging to crop species that the aid of Roman soldiers was sought to control the population. During the 17th century, Sir Francis Bacon noted in '*Sylva Sylvarum*' (1627) that the soil "that was brought out of the Indies and other remote countries for ballast for ships, cast upon some grounds in Italy, did put forth foreign herbs, to us in Europe not known". Early in the 20th century, in 'The Naturalisation of Animals and Plants in New Zealand', George M. Thomson (1922) asserted poor colonial land management facilitated species introductions. Ironically though, Thomson rejected the idea that introduced plants could inevitably displace native species.

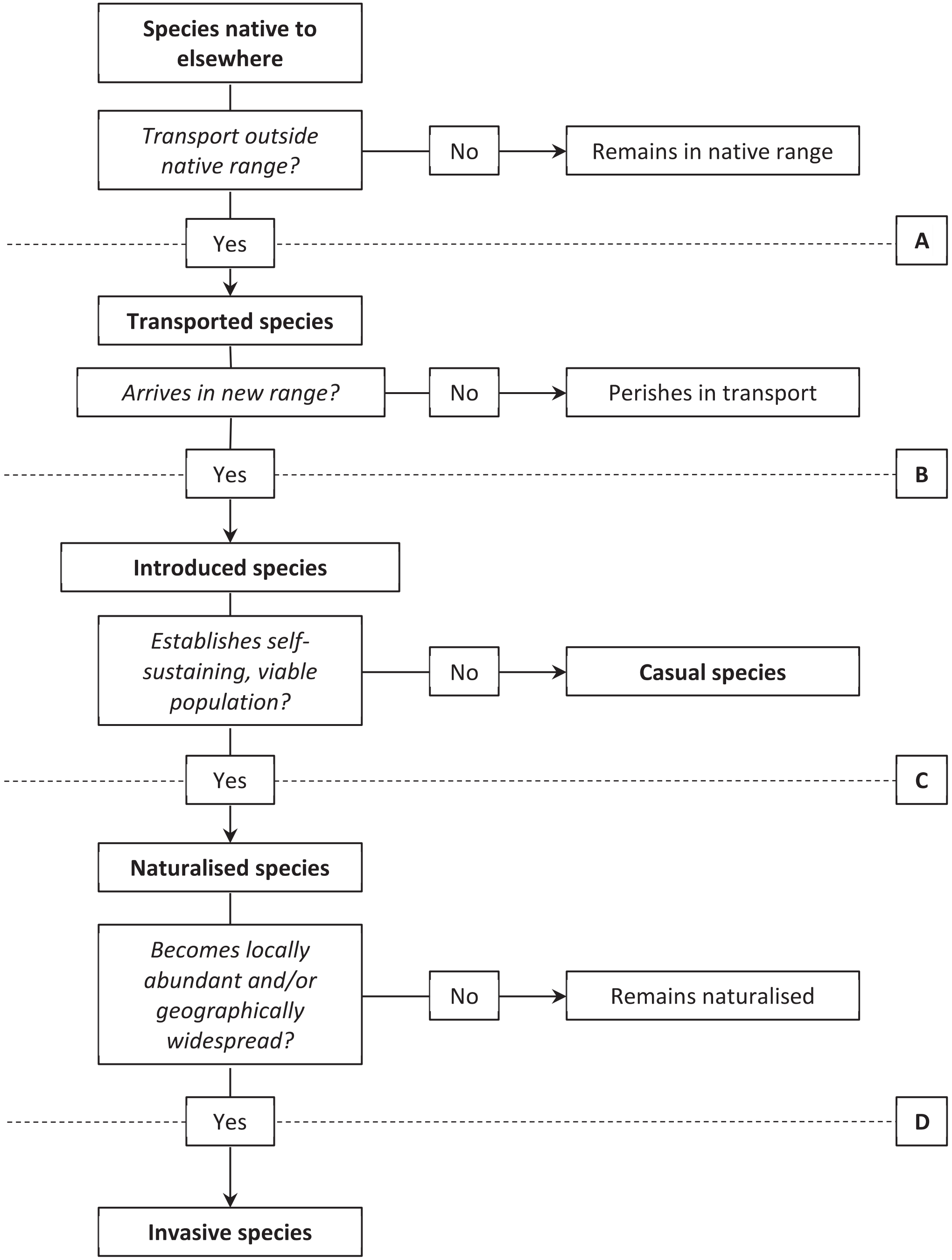
The scientific discipline known as "invasion ecology" which focuses on the ecology of invasive species was principally founded as a distinct research program by Charles Elton. In his post-World War II book '*The Ecology of Invasions by Animals and Plants'* (1958) Elton described "ecological explosions" of species growth, reproduction and geographic spread. Of species invasions, he said "they are so frequent nowadays in every continent and island, and even in the oceans, that we need to understand what is causing them and try to arrive at some general viewpoint about the whole business… We must make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora". Unravelling the causes of species invasions remains a central theme within modern ecological research. This is witnessed by the emergence of many dedicated scientific journals including *Biological Invasions*, *Diversity and Distributions*, *Neobiota* and *Weed Science*.

1.2.1 THE PROBLEM OF INVASIVE EXOTIC PLANT SPECIES

The introduction of exotic plant species into areas beyond their native range is increasing at a rapid rate (Pickard 1984, Richardson and Pyšek 2006, Wonham and Pachepsky 2006), mostly as a result of human activity (Lonsdale and Lane 1994, Vitousek *et al*. 1997, Pyšek and Jarošik 2005). Invasive exotic plant species have an array of negative ecological impacts on the biodiversity within the ecosystems they invade (Parker *et al*. 1999, Mack *et al*. 2000, Pyšek *et al*. 2008, Pyšek and Richardson 2010, McGeoch *et al*. 2010, Vilà *et al*. 2010). Studies have shown that these negative impacts are felt at many scales, from individuals and populations through to continental and global scales (Vitousek *et al.* 1996). Furthermore, the management and eradication of invasive exotic plant species can incur massive costs to economies (Perrings *et al*. 2000, Pimentel *et al*. 2005, Coutts-Smith and Downey 2006, Binimelis *et al*. 2007, Kettunen *et al*. 2009, Vilà *et al*. 2010). Understanding the drivers of species invasiveness is crucial for optimising invasive plant species management and prioritizing the eradication of problematic plant species (Richardson *et al*. 2000, Pyšek *et al*. 2008, Phillips *et al*. 2010a).

1.2.2 THE NATURALISATION TO INVASION TRANSITION

Scientific agreement as to what defines an invasive plant species has proved to be a challenging task, often leading to ambiguous terminology and confusion in both scientific literature and popular media (Williams and Meffe 1998). The carefully-crafted terminology outlined by Richardson *et al*. (2000) addressed this issue by identifying species invasiveness in the context of an ongoing ecological process of rapid geographic spread, rather than focusing solely on a species' direct impact on its surrounding environment. The 'invasion pathway' concept defines invasive species in the context of all other introduced species within a region (Box. 1; Modified from Lodge 1993, Richardson *et al*. 2000, Kolar and Lodge 2001, Sakai *et al*. 2001, Blackburn *et al*. 2009). The invasion pathway describes a species' progression through several stages, crossing several major geographic and ecological barriers on the path to becoming invasive (Box 1).



Box 1.1: The Introduction to Invasion Pathway

Exotic species must pass through several ecological and geographic barriers before becoming invasive within an introduced range. The category names for species are in bold font.

A horizontal dashed line indicates a barrier to be overcome along the pathway. Dichotomous possibilities at each barrier are posed as questions in italics.

Barrier ‘A’ represents extraction or escape from the native range.

Barrier ‘B’ represents surviving transportation across a geographic barrier (e.g. ocean, mountain range, desert) that the species could not cross naturally.

Barrier ‘C’ represents a species’ ability to persist in a novel range without human intervention.

Barrier ‘D’ represents a species’ ability to become locally abundant and/or spread geographically. The scale of spread reflects the scale of the invasiveness.

The transportation stage includes a species surviving extraction or escape from its native range (Barrier 'A') and transportation to the introduced range (Barrier 'B'). The transportation stage is facilitated by either accidental or deliberate movement of the species by humans across a geographic barrier (e.g. a mountain range or an ocean) that the species could not otherwise cross naturally.

The establishment stage, whereby a species naturalises and forms a self-sustaining population, requires a species to survive and endure within the introduced range without the intervention of humans (Barrier 'C'). Barriers which impede establishment could include incompatible climate, insufficient resources or the prevalence of predators in the new range. The invasive stage follows when a naturalised species is able to reproduce prolifically and spread rapidly across a wide geographic region (Barrier 'D'). Naturalised exotic plant species that become invasive can generate dramatic ecological changes that include reductions in native species richness and altered ecosystem function (Lockwood *et al*. 2007).

Although many exotic plant species become naturalised following their introduction into new regions, only a small subset of naturalised species go on to become invasive (Groves *et al*. 2005). This thesis examines the crucial naturalisation to invasion transition in the pathway and aims to identify factors that increase the likelihood of species becoming invasive among naturalised exotic plant species (i.e. crossing Barrier 'D' in Box 1).

1.3 THE VALUE OF TRAIT INFORMATION FOR UNDERSTANDING INVASIVENESS

A growing body of studies is gradually building evidence for the idea that variation among species in their traits is linked to interspecific differences in the likelihood of transitioning through the naturalisation to naturalisation pathway (e.g. Rejmánek 2000, Kolar and Lodge 2001, Sutherland 2004, Cadotte *et al.* 2006b, Pyšek and Richardson 2007). An emerging approach in invasion ecology is to focus on distinguishing trait variations among plant species that might be drivers of invasiveness, in part to improve predictive systems for invasive species management. There are two primary categories of traits that are relevant to the task of identifying consistent patterns of invasiveness in plants; introduction-history traits and life-history traits.

1.3.1 INTRODUCTION-HISTORY TRAITS

Introduction-history traits of species are attributes that relate to patterns of species introduction to a new region. Three examples of these traits include residence time in the introduced region (i.e. how long a species has been present in the introduced range), the reason that a species is introduced to that region (a simple distinction is between accidental and deliberate introductions) and the native range or continent of origin of the exotic species (Pikard 1984, Corlett 1992, Rejmánek 2000, Mack and Ernberg 2002, Wu *et al*. 2004, Castro *et al*. 2005, Hamilton *et al*. 2005, Pyšek and Jarošik 2005, Wilson *et al*. 2007, Harris *et al*. 2007).

1.3.2 LIFE-HISTORY TRAITS

Life-history traits of species relate to survival, establishment, growth and reproduction. Examples of life-history traits with the potential to drive species invasiveness include seed mass, germination and dispersal as well as maximum attainable canopy height, resistance to soil pathogens, leaf traits linked to photosynthesis and seedling growth (Crawley *et al*. 1996, Rejmánek 1996, Rejmánek and Richardson 1996, Williamson and Fitter 1996a,b, Reich *et al*. 1997, Sakai *et al*. 2001, van Clef and Styles 2001, Hampe 2004, Hamilton et al. 2005, Lloret *et al*. 2005, Pyšek and Richardson 2007, Ordonez *et al*. 2010, Säumel and Kowarik 2010).

In this thesis, I employ a trait-based approach to determine critical aspects of trait variation among plant species related to introduction history and life history that are likely to drive species invasiveness among the naturalised exotic flora found in Australia.

1.4 THE 'TARGET-AREA' APPROACH: APPLICATION TO AUSTRALIA

The analysis of datasets comprising large numbers of species that have been assembled by implementation of the 'target-area' approach has been shown to be an informative methodology for determining plant traits linked to the shift from naturalisation to invasion (Pyšek *et al*. 1995, Cadotte *et al*. 2006b). By comparing the pool of naturalised non-invasive species with the pool of naturalised invasive species in the introduced region (i.e. the target area), broad patterns of ecological generality have emerged about plant traits linked to invasiveness. For instance, a recent analysis of a large dataset of naturalised plant species in Ireland revealed that species introduced for ornamental purposes were more likely to be invasive (Milbau and Stout 2008). In a macroecological study using the introduced flora of China, 68% of the 126 exotic plant species categorised as invasive within the country were found to have originated in the continents of North and South America (Liu *et al*. 2006). The work presented in my thesis is the first to employ such a target-area approach to examine species invasiveness within the naturalised exotic flora of Australia at a continental scale.

Australia is a unique island continent in that it is entirely isolated from other continents by vast distances of ocean. This isolation severely restricts natural animal and plant dispersal to and from other regions and creates unique floral and faunal communities. It is a geologically ancient continent, approximately 7.6 million km^2 in total land surface area, which contains a great spectrum of ecosystem types that have formed over millions of years, including arid deserts, grasslands, sclerophyll woodlands, alpine regions, rainforests and coastal wetlands. Many parts of Australia are typified by environmental resource paucity, including low seasonal rainfall and poor soil nutrient availability. Considered together, all of these characteristics of Australia make it a unique system with which to test macroecological patterns and processes (Murray *et al*. 1998). Importantly, the comparatively recent permanent settlement by Europeans beginning in 1770 has seen Australia's human population grow to over 22,500,000 people (March 2011, abs.gov.au). Population modelling by Johnson and Brook (2011) has estimated that prior to this, Australia's Aboriginal population was about 1,000,000 people.

An assessment from the National Land and Water Resources Audit released in 2004 calculated that, since permanent European settlement in 1788, over 700,000 km^2 of woodland and forest, 130,000 km^2 of mallee, 20,000 km^2 of heathland and 60,000 km^2 of tussock grasslands have been cleared or heavily thinned, primarily for agricultural planting and animal grazing. Generally, ecosystems found on the most fertile soils have suffered the highest levels of ecological modification, and up to 90% of the total original native habitat which existed in the eastern temperate zone of Australia has now been entirely cleared of endemic flora and fauna.

Along with the current vast expanse of highly-modified and continually-disturbed environments and the increasing human population, the introduction of new species has occurred on a massive scale, with many thousands of new species introduced to Australia both intentionally (for anthropocentric reasons) and unintentionally (through transport contamination for example) after colonial settlement. Approximately 27,000 new plant species have been brought in to Australia over the last three centuries, with 2,739 plant species known to have formed naturalised populations in the natural environment and over 130 plant species known to have become invasive within Australia (Randall 2007). Since European settlement began in earnest in 1770, invasive exotic plant species native to many regions of the world (both near to and far from Australia) have arrived in Australia (Murray and Phillips 2012).

The economic costs associated with managing and eradicating invasive plants in Australia surpasses $4 billion each year, with much of this invested in managing invasive species that have an impact on agricultural industries (Martin 2003). A total of $1 in every $7 of agricultural income is spent on eradicating and mitigating the impacts of invasive plants (Sinden *et al*. 2004). In the state of New South Wales, invasive plants have been identified as the second biggest threat to biodiversity following land clearing (Coutts-Smith and Downey 2006). At least four Australian plant species are known to have become extinct as a direct result of resource competition with invasive species (Leigh and Briggs 1992). Unlike elsewhere in the world, where patterns of exotic plant invasiveness have been the focus of enormous research effort (e.g. Central Europe, Pyšek *et al*. 1995, Pyšek *et al*. 2003, Krivanek and Pyšek 2006, Lambdon *et al*. 2008, Chytry *et al*. 2009, Pyšek *et al*. 2009), there is a comparative paucity of information concerning such patterns and processes for Australia. While a growing body of work over the last 20 years is beginning to raise the importance of understanding the patterns and processes in exotic plant invasions for Australian ecosystems (e.g. Lonsdale 1994, Groves and Hosking 1998, Lake and Leishman 2004, Groves *et al*. 2005, Hamilton *et al*. 2005, Leishman *et al*. 2007, Leishman *et al*. 2010, Murray and Phillips 2010, Phillips *et al*. 2010a), unfortunately, we are yet to possess as comprehensive an understanding of exotic plant invasiveness in Australia as has been developed for other regions of the world.

1.6.1 RESEARCH OVERVIEW

The research presented in this thesis is based on the concept of the introduction to invasion pathway, with a specific focus on the naturalisation to invasion transition (Box 1.1). By focusing on this transition, I aim to identify traits linked to the invasive geographic spread of naturalised exotic plant species. The work in this thesis employs the target-area approach for Australia and considers patterns of exotic species invasiveness at a continental scale. In this context, I develop a novel framework for species selection in order to provide the most meaningful way of comparing traits between invasive and non-invasive species. Central to this framework is a complementary approach using both classical statistical tests as well as recently-developed approaches for considering the phylogenetic relatedness of species (i.e. 'phylogenetically-independent contrasts'). I seek to identify plant introduction and life-history traits that distinguish invasive from non-invasive species. I perform desktop studies and a series of manipulative experiments to test predictions relating these traits to exotic species invasiveness. My experiments span the seed-bank and seed germination stages to seedling establishment and growth stages.

1.6.2 THESIS OBJECTIVES

Four main objectives are addressed in this thesis:

1. To determine relationships between introduction-history traits and species invasiveness among exotic plants introduced to Australia by humans since the beginnings of permanent European settlement.
2. To create a framework for species selection in mensurative and manipulative experiments designed to identify life-history traits underpinning invasiveness.
3. To quantify relationships between life-history traits and species invasiveness.
4. To understand the role that biotic and abiotic ecological attributes, including soil-borne pathogens and soil nutrient enrichment, play in determining the invasion success of exotic plant species.

1.6.3 THESIS STRUCTURE

I address the objectives of this thesis with the following chapter structure:

Chapter 2 describes a desktop study that identifies relationships between introduction-history traits and species invasiveness among naturalised exotic plant species occurring in Australia. This chapter has been published as a peer-reviewed manuscript: Phillips M.L., Murray B.R., Leishman M.R. and Ingram R. (2010) The naturalization to invasion transition: are there introduction-history correlates of invasiveness in exotic plants of Australia? *Austral Ecology,* 35: 695-703.

Chapter 3 details a follow-on desktop study that quantifies relationships between plant life-history traits and species invasiveness among naturalised exotic plant species occurring in Australia. I used the findings of Chapter 2 to develop a framework for species selection to construct the most meaningful analysis of species invasiveness within the naturalised exotic flora found in Australia. This framework is the central model for species selection within the subsequent chapters of this thesis. In addition, I adopted a complementary approach of both cross-species and phylogenetic analyses (in this case correlated-divergence analysis) to unravel the evolutionary underpinnings of present-day relationships between life-history traits and species invasiveness.

In Chapter 4, I present an experimental comparison of seed survival in the soil of the introduced range between congeneric invasive and non-invasive species using a common-garden field experiment (i.e. where individuals from different localities are raised under the same natural conditions in a field setting). I used multiple congeneric contrasts, employing the species selection framework established in Chapter 3, spanning a wide range of taxonomic families (this approach is also adopted in the following two chapters). In particular, I experimentally test the hypothesis that seeds of non-invasive species are more vulnerable to seed mortality from pathogenic soil-borne fungi than seeds of invasive species. Here, and in the following two chapters, I employed a general / generalized linear modelling approach to analyse my field data as this approach could incorporate within-species variation (i.e. replicates) in seed survival. In this case, phylogenetic relationships among species were explicitly considered through (i) species selection and (ii) the inclusion of taxonomic information (at the level of genus) in generalized linear models. This chapter is currently in press as a peer-reviewed manuscript: Phillips M.L. and Murray B.R. (2011) Invasiveness in exotic plant species is linked to high seed survival in the soil. *Evolutionary Ecology Research*.

Chapter 5 presents the results of a laboratory-based experiment that explored a range of seed germination traits and their relationships with species invasiveness.

In Chapter 6, I present the results of a glasshouse experiment designed to compare seedling growth between congeneric invasive and non-invasive plant species. In particular, I test whether soil nutrient enrichment differentially affected seedling emergence and growth traits of invasive and non-invasive species.

Chapter 7 presents the results of an international collaboration examining the introduction of exotic plant species from the Central European flora to Australia. Although this work does not specifically target the naturalisation to invasion transition, it provided a unique opportunity to explore naturalised plant species in Australia and their temporal patterns of introduction. This chapter has been published as a peer-reviewed manuscript: Phillips M.L., Murray B.R., Pyšek P., Pergl J., Jarošik V., Chytrý M. and Kühn I. (2010b) Plants species of the Central European flora as aliens in Australia. *Preslia*, 82: 465-482.

Chapter 8, the final chapter of the thesis, provides an overall synthesis of the findings of each chapter and how these findings collectively further our understanding of exotic plant species invasiveness in Australia. This chapter concludes with a discussion of potential future research directions arising as a result of the findings of this thesis.

Chapter 2

The naturalisation to invasion transition: Introduction-history correlates of invasiveness in the exotic flora of Australia

This chapter has been published as: Phillips M.L., Murray B.R., Leishman M.R. & Ingram R. (2010) The naturalization to invasion transition: Are there introduction-history correlates of invasiveness in exotic plants of Australia? *Austral Ecology*, 35: 695-703.

2.1 INTRODUCTION

The introduction of exotic plants into new geographic regions as a result of human activities is recognized as a serious threat to global biodiversity and as a major component of global change (Lövei 1997, Ewel *et al*. 1999, Adair and Groves 1998, Sala *et al*. 2000, Millennium Ecosystem Assessment 2005, Ricciardi 2007). Exotic plants that naturalise and become invasive can generate dramatic ecological changes that include reductions in native species richness and altered ecosystem function (Elton 1958, D'Antonio and Vitousek 1992, Brooks *et al*. 2004, Gerber *et al*. 2008, Hejda *et al*. 2009, Robson *et al*. 2009). At the same time, however, biological invasions present many opportunities as a set of unplanned experiments to test ecological theory (Inderjit 2005, Sax *et al*. 2005, Cadotte *et al*. 2006a, Sax *et al*. 2007). Given that invasive species are distinguished by their spread, high abundance and wide distribution, an understanding of the factors underpinning the success of invasive species has the potential to shed further light on characteristics that separate rare from common species (Murray *et al*. 1999, Murray and Westoby 2000, Murray *et al*. 2002, Murray and Lepschi 2004).

An exotic species becomes invasive when it escapes the condition of being naturalised in a new region and spreads widely and in high abundance (Richardson *et al*. 2000). Many exotic plant species become naturalised following their introduction into new regions, however, only a small subset of these naturalised species go on to become invasive (Williamson and Fitter 1996, Groves *et al*. 2005, Caley *et al*. 2008). Identifying the factors that drive invasiveness among species has been a central goal of invasion ecology for many years (Baker 1965, Pyšek *et al*. 1995, Rejmánek 1996, Reichard and Hamilton 1997, Kolar and Lodge 2001, Booth *et al*. 2003, Cadotte *et al*.

2006b, Pyšek and Richardson 2007, Dawson *et al*. 2009). Despite some concern that generalizations are unlikely to emerge (Moles *et al*. 2008), recent research is revealing important insights into the general characteristics of invasive plant species and is critical for efforts directed towards the pre-emptive targeting of invasive species (Scott and Panetta 1993, Pheloung *et al*. 1999, Wittenberg and Cock 2001, Křivánek and Pyšek 2006, Pyšek and Richardson 2007).

2.1.1 THE TARGET-AREA APPROACH: AUSTRALIA

An informative methodology for determining plant attributes linked to the transition from naturalisation to invasion is the analysis of datasets comprised of large numbers of species that have been assembled by implementation of the 'target-area' approach (Pyšek *et al*. 1995, Pyšek *et al*. 2004, Cadotte *et al*. 2006b). By comparing the pool of naturalised non-invasive species with the pool of naturalised invasive species in the introduced region (i.e. the target area), broad patterns of ecological generality can emerge about plant attributes linked to invasiveness (Hamilton *et al*. 2005). This approach differs from the 'source-area' approach which addresses whether life histories of species that become invasive from a given geographic source region differ from those species that do not invade from that same source region (Prinzing *et al*. 2002).The target-area approach is also different from the 'native-comparison' approach which compares the life-history traits of native with non-native species in the new environment (Crawley *et al.* 1996, Cadotte and Lovett-Doust 2001, Lake and Leishman 2004, Leishman and Thomson 2005). This approach addresses whether the traits of invading species enhance their potential to increase in abundance over native species.

The first step in any target-area study is to identify correlates of invasiveness that comprise elements of the introduction histories of species (Harris *et al*. 2007). There have been a small number of attempts throughout different regions of the world to identify links between introduction to invasion patterns of exotic plant species and introduction-history traits (Rozefelds *et al*. 1999, Vilà and Pujadas 2001, Pyšek and Jarošík 2005, Lambdon and Hulme 2006, Milbau and Stout 2008, Dawson et al. 2009). Australia is particularly vulnerable to exotic plant invasion due to its isolation and unique biota and few ecosystems in Australia are immune to invasion (Adair and Groves 1998, Groves and Hosking 1998, Groves *et al*. 2005). Thus, Australia provides an important test of macroecological patterns (Murray *et al*. 1998) especially those relating to introduction history and invasion success among a large pool of species. Key traits in this context include the geographic origin of species, their reason for introduction, how long species have been present in the new region, the taxonomic membership of introduced species and interactions between these traits and plant growth form. Very little is known, however, about whether these attributes are linked explicitly to the most problematic phase of the introduction to invasion pathway, the shift from naturalisation to invasion (Richardson *et al*. 2000).

To address the paucity of information on the effects of introduction-history attributes on the shift from naturalisation to invasion, a large dataset of naturalised plant species in Australia was compiled and introduction-history traits were compared between naturalised non-invasive species and naturalised invasive species. A focus on the naturalisation to invasion transition was specifically chosen for two important reasons. First, it is absolutely crucial to investigate each stage of the introduction to invasion pathway separately, because the relative importance of a range of factors varies at different stages along the invasion pathway (Lloret *et al*. 2004, Dietz and Edwards 2006, Diez *et al*. 2008, Dawson *et al*. 2009). Second, the transition from naturalisation to invasion represents the critical step where species escape the naturalised state to become invasive and at the latter stage can become serious ecological, economic and social problems (Lockwood *et al*. 2007).

2.1.2 RESEARCH QUESTIONS

In the present study, data were gathered on continent of origin, reason for introduction, minimum residence time, growth form and taxonomy for all species within the dataset. Here, no *a priori* predictions are made as to relationships between invasion success and introduction method or continent of origin, but nevertheless, identification of particular reasons for introduction or source regions for exotic flora linked to invasiveness can provide useful information for predictive models for potentially invasive species (Prinzing *et al*. 2002). Using the species introduction-history data, the following questions were asked:

(i) Are residence times of invasive species in Australia significantly longer on average than residence times of non-invasive species?

(ii) Do invasive and non-invasive species differ significantly as a function of reason for introduction?

(iii) Are there particular plant growth forms that are more likely to be invasive than others?

(iv) Do invasive and non-invasive species differ significantly in relation to continent of origin?

2.2 METHODS

2.2.1 INTRODUCTION-HISTORY TRAITS

Residence time refers to the period of time that an exotic species has been present in a new region outside its native range (Pyšek *et al*. 2004). Longer residence times have been linked to species invasiveness in a number of studies (Rejmánek 2000, Castro *et al*. 2005, Pyšek and Jarošík 2005, Harris *et al*. 2007, Wilson *et al*. 2007). Longer residence times may provide exotic plant species with enough time to establish and spread and thus overcome any 'lag' period (Sakai *et al*. 2001). Furthermore, residence time is an important component of propagule pressure (Richardson and Pyšek 2006). The longer time that a species is present in a region, the more propagules it is able to produce and disperse, key components of invasiveness for exotic plants (Küster *et al*. 2008), therefore we may predict that Australian invasive plant species will have on average longer residence times than non-invasive species. In a broad context, exotic plant species arrive in new regions via one of three main pathways, as ornamental, agricultural or accidental introductions (Pickard 1984, Mack 2001, Mack and Erenberg 2002, Wu *et al*. 2004, Milbau and Stout 2008). Exotic plants may also arrive in a new region from a variety of different geographical regions. Indeed, exotic plants may flourish in climatically similar areas to that of their native range (Corlett 1992, Wu *et al*. 2004), which suggests that similar environmental conditions may be an important determinant of invasion success. At the same time, however, given a strong link between Australia and England as a result of permanent settlement just over 200 years ago, there may be a link between invasion success and the European origin of plant species.

2.2.2 STUDY SPECIES AND DATASET COMPILATION

A dataset of all naturalised invasive and naturalised non-invasive plant species was compiled using information from the latest compendium of the introduced flora of

Australia (Randall 2007).This compendium not only comprehensively lists all naturalised non-invasive plant species in Australia (species listed with just the category 'N'), it also identifies which species are classified as invasive across Australia (category '5A' species). The separation of species into two clearly defined categories (invasive species n = 133, non-invasive species n = 335) allows us to better understand the nature of the relationships between introduction-history attributes and the transition from the state of naturalisation to the state of invasion.

The compiled dataset contained a total of 127 taxonomic families. The five most speciose families were *Poaceae, Leguminosae, Asteraceae, Lamiaceae* and *Rosaceae*. A χ^2 contingency test showed that there was no significant difference ($\chi^2 = 3.99$, d.f. = 4, P = 0.55) between the proportions of invasive and non-invasive species in these five families (the inclusion of other families in the analysis was precluded as expected values in the contingency analysis were <5 and thus assumptions of the statistical test were violated). Given that the dataset was comprised of a wide variety of families, there was no over-representation of invasive species in the five largest families, and that the primary interest was in contemporary patterns in the present-day assemblage of species (i.e. not specifically asking evolutionary questions), the analyses of species data focussed on a cross-species approach (Westoby *et al*. 1998, Clarke 2002).

The Department of Agriculture, Fisheries and Forestry Census of Cultivated Plants 2009 provided data on the earliest year of introduction for each species. Minimum residence time for each species was calculated as the current year (2009) minus the earliest year of introduction (see Hamilton *et al*. 2005). Public domain sources including over 600 Plant Nursery Catalogues spanning 200 years, Botanical and major Garden plant species lists, Australian Quarantine and Inspection Service permitted import list, State Department vegetation surveys and Commonwealth lists of imported species were meticulously sourced for these data. Growth form and continent of origin data were obtained from a wide range of sources including continental and regional floras, online databases and herbarium records.

2.2.3 STATISTICAL ANALYSES

Differences between the proportions of invasive and non-invasive species originating from each continent (South America, North America, Europe, Australasia and Africa) were examined using a χ^2 contingency test. Logistic regression was used to compare minimum residence times between invasive and non-invasive species, with residence time calculated as the current year (2009) minus the year of introduction. A two-way ANOVA was used to determine whether there were significant differences in residence time as a function of both invasion success and continent of origin.

Differences between the proportions of invasive and non-invasive species introduced to Australia as ornamental plants (introduced for horticultural and aesthetic purposes), agricultural plants (brought to Australia for the purposes of edible pastures, stock and forestry) or as unintentional releases (e.g. contamination of ballast and grain as well as other unplanned incursions) were analysed using a χ^2 contingency test. Differences between the proportions of invasive and non-invasive species in each primary growth form category (herb, shrub, tree, climber) were examined using a χ^2 contingency test. Statistical analyses were performed in GLIM (version 3.77, Royal Statistical Society, London) and significant differences reported at the level of $P < 0.05$.

2.3 RESULTS

The proportions of invasive and non-invasive species originating from each continent differed significantly ($\chi^2 = 57.50$, d.f. = 4, $P < 0.0001$). More invasive species than expected originated from South America and North America, while fewer invasive species than expected originated from Europe and Australasia (Fig. 2.1). Species from Africa were just as likely to be invasive as non-invasive. There was no significant difference ($\chi^2 = 1.25$, d.f. = 2, $P = 0.54$) between invasive and non-invasive species with respect to reason for introduction to Australia (Fig. 2.2). Invasive species were significantly more likely to have been resident in Australia for a longer period of time than non-invasive species ($\chi^2 = 20.48$, d.f. = 1, $P < 0.0001$; Fig. 2.3). Fewer invasive species than expected were herbs and more invasive species than expected were climbers (Fig. 2.4). Residence times of invasive species were consistently and significantly higher than residence times of non-invasive species even when each continent was considered separately (Fig. 2.5). Furthermore, overall residence times varied significantly as a function of continent of origin, with species from South America having been introduced to Australia more recently on average than species from Europe, Australasia and North America (Student's t posthoc tests, $P < 0.05$; Table 2.1, Fig. 2.5). The proportions of invasive and non-invasive species within each growth form category differed significantly ($\chi^2 = 45.\ 31$, d.f. = 3, $P < 0.0001$).

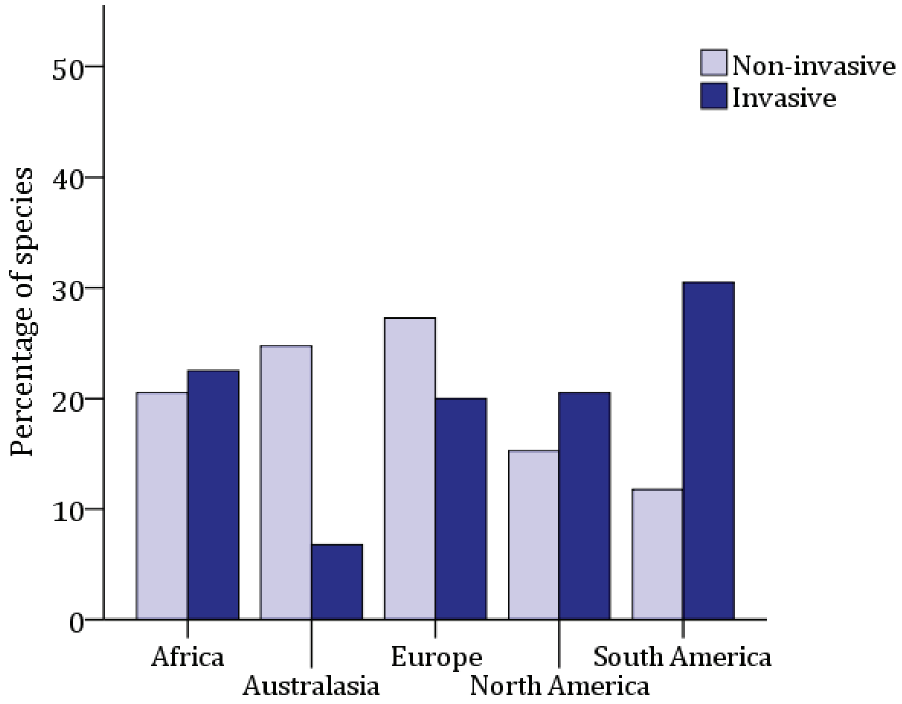


Figure 2.1. The percentage of naturalised invasive and non-invasive exotic plant species in Australia originating from different continents.

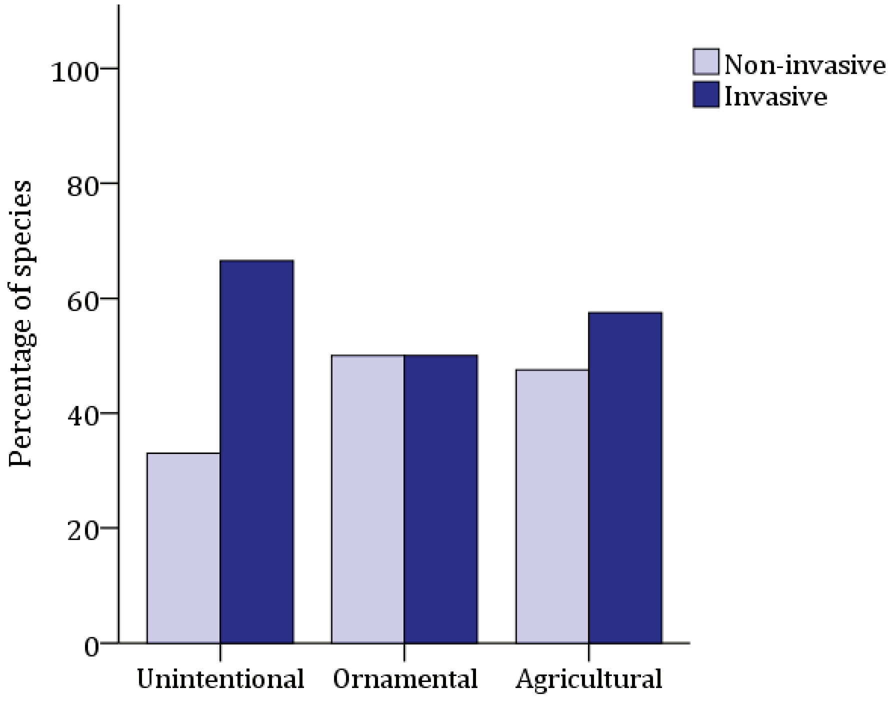


Figure 2.2. The percentage of naturalised invasive and non-invasive exotic plant species introduced into Australia unintentionally or for ornamental or agricultural purposes.

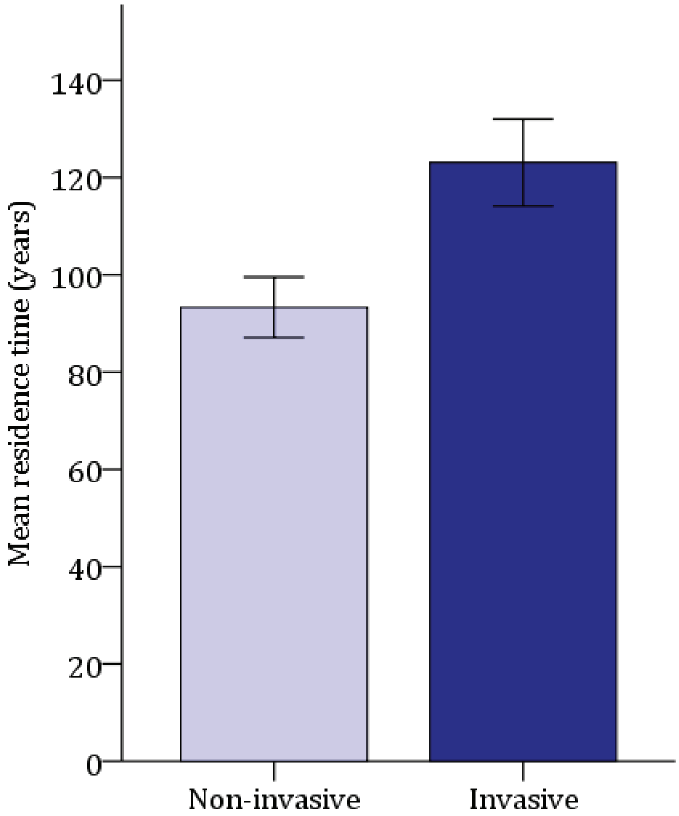


Figure 2.3. Residence times (mean ± SE) of naturalised invasive and non-invasive exotic plants in Australia.

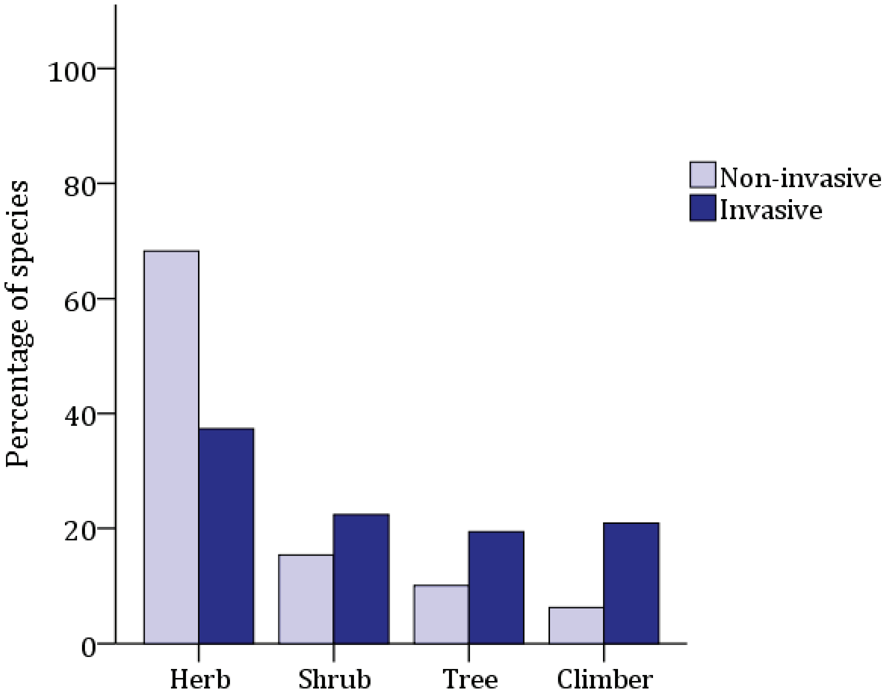


Figure 2.4. The percentage of naturalised invasive and non-invasive exotic plant species in Australia in each primary growth form

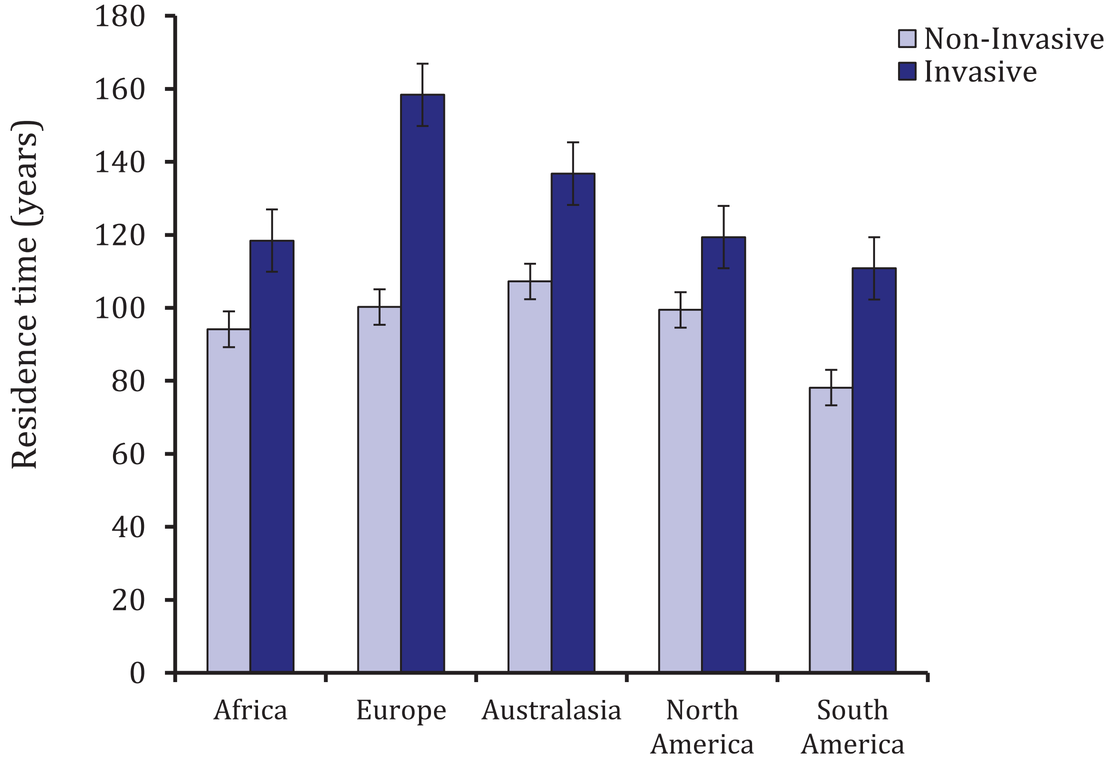


Figure 2.5. Residence times (mean ± SE) of naturalised invasive and non-invasive exotic plants in Australia as a function of continent of origin.

Table 2.1. Two-way ANOVA examining differences in residence time (response variable) as a function of both invasion success (two-level explanatory variable, invasive and non-invasive) and continent of origin (five-level explanatory level, South America, North America, Europe, Australasia and Africa).

	F	d.f.	*P*
Invasion	40.56	1, 719	< 0.0001
Continent	3.24	4, 719	0.01
Invasion x continent	1.09	4, 719	0.36

2.4.1 DISCUSSION

Significantly longer residence times were observed among invasive plant species in Australia compared with non-invasive species. The observed link between long residence time and invasion success conforms to patterns emerging elsewhere in the world (Rejmánek 2000, Pyšek *et al*. 2003, Wu *et al*. 2003, Harris *et al*. 2007, Milbau and Stout 2008). Longer residence times are probably linked to invasiveness because they allow exotic plant species to take time to establish and spread sufficiently in order to overcome a ‘lag’ period (Sakai *et al*. 2001). This is particularly relevant in the case of ‘sleeper’ weeds (Groves 1999), a sub-group of invasive plant species whose population sizes are known to have increased significantly at least 50 years after they have become naturalised. For example, *Mimosa pigra* was planted in the Darwin Botanic Garden around 1891 (Miller and Lonsdale 1987), but it wasn’t until 1952 when it was relocated to the headwaters of the Adelaide River that it became a major invasive species (Groves 2006). Furthermore, residence time is an important component of propagule pressure (Richardson and Pyšek 2006). The longer time that a species is present in a region, the more propagules it is able to produce and disperse, key components of invasiveness for exotic plants (Küster *et al*. 2008).

Invasive species had longer residence times on average than non-invasive species even when each continent of origin was considered separately. What is particularly interesting in our study is that invasive species from South America have been resident in Australia for a significantly shorter length of time than their counterparts from other continents including Europe, Australasia and North America (Fig. 4). Yet, these analyses also revealed that significantly more invasive species than expected have originated from South America. Put together, these findings support the claims that exotic species from different regions of the world should be treated separately in analyses employing the target-area approach (Pyšek *et al*. 2004). Residence times are important, but more so when comparing between invasive and non-invasive species originating from a particular continent. An important outcome of this finding is that exotic plant species from South America should probably be a priority concern, given that they appear in general capable of more rapid shifts to invasiveness than exotic plants from other regions. This is probably facilitated by aliens from South America being more suitably pre-adapted to the new environment (Sakai *et al*. 2001) in Australia, at least more so than species from the colder regions of Europe which have arguably had longer times to become invasive.

The key finding that a higher proportion of invasive than non-invasive species were climbers highlights the problematic nature of introducing climbing plant species to Australia. Climbing plants are undoubtedly successful invaders given that they can spread comparatively quickly and smother native vegetation in the process. For example, *Thunbergia grandiflora* has been shown to smother rainforest in north-east Australia at a rate of approximately 0.5 ha per year (van Haaren and Vitelli 1997). Recent work has illustrated that a total of 179 exotic climbing plant species from 40 families have been introduced to Australia since permanent settlement in 1788 (Harris *et al*. 2007). This is of great concern given that exotic climbers are thought to be one of the most destructive plant functional groups in an ecological context (Humphries *et al*. 1991). Surprisingly, there are few published studies of the ecological impacts of climbers (but see Ogle *et al*. 2000, Phillips *et al*. 2002, Yurkonis and Meiners 2004). Studies that address quantitatively the ecological impacts of exotic climbing plants are needed to assist in their control and in the protection of native fauna and flora.

The proportions of invasive and non-invasive species introduced as ornamentals, agricultural plants or as accidental incursions did not differ significantly for our Australian dataset. This might be expected given that plant species occur in these categories based on human values (e.g. aesthetics for ornamental plants) and usage, often with little bearing on plant species reproduction or function (i.e. biological features that might drive invasiveness). It may be argued, however, that the categories of reason for introduction used in this study were too broad to discern links between invasion success and reason for introduction. Obtaining historical data on more exact reasons for introduction is difficult. However, several studies have highlighted the importance of propagule pressure linked to the ornamental plant trade for naturalisation and invasiveness (Thuiller *et al*. 2005, Dehnen-Schmutz *et al*. 2007). The popularity of ornamentals can lead to a higher influx of seeds of ornamental exotic species, which can then lead to invasive spread (Milbau and Stout 2008). This suggests that further investigation of plant propagule pressure and its inherent links with reason for introduction is warranted.

2.4.2 CONCLUSIONS

A growing body of research is unravelling the factors underpinning the movements of species along the introduction to invasion pathway and important findings about relationships between invasiveness and life-history traits are emerging (Strauss *et al*. 2006, Ashton and Lerdau 2007, Herron *et al*. 2007, Jogesh *et al*. 2008, Cadotte *et al*. 2009, Dawson *et al*. 2009).The findings of such studies are important for assisting in the control of exotic plants because detection of species traits that are linked to invasion success is vital for pre-emptive management targeting potentially detrimental invaders (Keller *et al*. 2007). These results show that comparative analyses that explore life-history and ecological trait relationships with invasion success will be more informative if variation in introduction-history attributes (continent of origin, minimum residence time and growth form) is taken into account first. For example, the timing of commencement of flowering is a known correlate of residence time among aliens of the Czech Republic, with species capable of early flowering more prevalent among early introductions (Pyšek *et al*. 2003). Without careful studies designed to highlight such relationships, flowering time itself might have been thought an important correlate of invasiveness, rather than acknowledged primarily as a secondary correlate of invasiveness through its relationship with residence time. Thus, while obtaining historical information on the introduction of plants to new regions by human activities is often frustratingly difficult, it is absolutely necessary to make a concerted effort to acquire such data in order to tease apart the factors that contribute to the transition from naturalised to invasive in plants introduced to novel environments.

2.4.3 CODA

As a result of this paper being published in *Austral Ecology* in 2010, I was approached by international colleagues to work on a project examining the introduction of exotic plant species from the Central European flora to Australia. While this work was not specifically targeting the naturalisation to invasion transition, it provided an opportunity to explore naturalised plant species in Australia and their temporal patterns of introduction. I present this work in Chapter 7 of this thesis.

Chapter 3

The role of plant life-history traits in the naturalisation-invasion transition: a framework and Australian case study

3.1 INTRODUCTION

In this chapter, I examine relationships between species invasiveness and plant life-history traits. The first part of the chapter establishes a framework for the identification of life-history traits correlated with species invasiveness. I highlight the importance of using a complementary approach that combines 'cross-species' and 'phylogenetically-independent contrasts' methods of analysis. In particular, the framework specifies the setting up of congeneric contrasts between closely-related invasive and non-invasive species for mensurative and manipulative experiments. I then describe methodological issues to be considered in species selection at the experimental design stage of this complementary approach. In the second part of the chapter, I use the framework in a desktop case study aimed at determining relationships between species invasiveness and plant life-history traits for naturalised exotic plant species in Australia.

3.2 SPECIES SELECTION FRAMEWORK

3.2.1 QUANTIFYING INTERSPECIFIC TRAIT RELATIONSHIPS IN PLANT ECOLOGY

Ecological datasets comprising few to many species are often used to examine interspecific relationships between plant traits. For instance, Murray and Gill (2001) examined the relationship between fruit size and tree size across 362 Australian eucalypt species; Wright *et al*. (2006) examined coordination between leaf and stem traits of 175 evergreen species; and Sterk *et al*. (2006) examined the relationship between leaf traits and growth-survival traits of 50 sympatric tree species from a Bolivian rainforest. Such studies quantify relationships by considering each species as a statistically-independent data point in analyses, without any *a priori* consideration of phylogenetic relationships among the species in the dataset. Fundamentally, this 'cross-species' method of analysis (hereafter referred to as the 'CS' method) describes relationships among contemporary species that are functionally important and are being maintained under continuing environmental selection pressures (Westoby *et al*. 1998, Cadotte *et al*. 2006).

Another way to quantify interspecific relationships between plant traits is to explicitly consider the phylogenetic relatedness of species in statistical analyses. The use of a 'phylogenetically-independent contrasts' method (hereafter referred to as the 'PIC' method) treats each node within the species phylogeny as a statistically-independent data point in analyses (Ridley 1983, Felsenstein 1985, Grafen 1989, Harvey and Pagel 1991). In the simplest case, the value at a node from which two species diverge is calculated as the difference in trait values between the two species diverging from that same node (Felsenstein 1985, Martins and Hansen 1996). The important feature here is that values determined for nodes are statistically independent units when they describe separate radiations in a phylogenetic tree. Node values can be used in place of trait values of species to perform PIC analyses in a variety of statistical techniques, including correlation, regression and principal components analysis (Felsenstein 1985, Garland *et al*. 1999).

The PIC method has been applied across a wide range of ecological datasets (e.g. Weathers and Seigel 1995, Edwards and Westoby 1996, Mack 1996, Swanborough and Westoby 1996, Wolf *et al*. 1998, Nicotra *et al*. 2002, Hoffman and Franco 2003, Cassey *et al.* 2004). The simplest application of the PIC method starts by pairing two closely-related species that contrast with each other in a trait of interest. For example, a rare species might be contrasted with a common species within the same genus (here, rarity or commonness is considered a dichotomous plant trait), or a drought-tolerant species might be contrasted with a drought-susceptible congener (here, drought tolerance is considered a dichotomous plant trait), to examine potential differences in other life-history traits (either categorical or continuous) related to the initial contrast. As an example of this approach, Murray and Westoby (2000) established two pairs of phylogenetically-contrasted rare and common plant species and found that seed output in the common species was ten-times larger than the contrasted rare species in each contrast. This study provided robust evidence for independent correlated divergences between rarity and low seed output (and between commonness and high seed output) in two separate phylogenetic radiations. Such pairings are phylogenetically independent because they are based on independent evolutionary divergences in a phylogeny (Felsenstein 1985, Harvey and Pagel 1991). The idea of using more than one contrast is that one can detect whether evolutionary divergences in one trait (e.g. rarity) are correlated with divergences in another trait (e.g. seed output) on one, multiple or no occasions throughout many divergences in a phylogeny.

3.2.2 A COMPLEMENTARY ‘CS’ AND ‘PIC’ APPROACH

It has been argued that the PIC method should supersede a cross-species approach due to issues of statistical non-independence thought to permeate traditional cross-species analyses (e.g. Harvey *et al*. 1995a,b, Rees 1995). However, the case has also been made that the key strength of the PIC method is that it can be used to specifically address evolutionary questions about trait relationships (Westoby *et al*. 1995a,b,c, Westoby *et al*. 1998). Here, I take the position that the use of both CS and PIC methods in a complementary fashion can yield valuable insights into the evolutionary underpinnings of present-day functional relationships between traits. For example, Maherali *et al*. (2005) used CS and PIC analyses on a set of 167 species from 50 seed plant families and examined relationships among resistance to xylem cavitation, water transport capacity and climate in order to examine the adaptive significance of resistance to water-stress-induced xylem cavitation for desiccation tolerance. The CS analysis revealed that across all plant species, cavitation resistance increased with decreasing mean annual precipitation. However, significant PIC correlations between resistance to cavitation and annual precipitation were found within the evergreen angiosperms and conifers but not in the deciduous angiosperms. This means the adaptive significance of increased resistance to cavitation as a mechanism of drought tolerance may be of primary importance in evergreen angiosperms and conifers, rather than all plant species as the CS analysis initially indicates. The strength of using complementary CS and PIC analyses in this example is that the PIC analysis was able to reveal what part of the phylogeny was driving the significance detected by the CS analysis.

3.2.3 A COMPLEMENTARY ‘CS’ AND ‘PIC’ APPROACH FOR INVASION ECOLOGY

In invasion ecology, a growing number of studies have discussed the role of phylogeny in deepening our understanding of how plant traits relate to plant species invasiveness (Rejmánek 1995, Mack 1996, Grotkopp *et al.* 2002, Pyšek *et al*. 2004, Muth and Pigliucci 2006, Jeschke and Strayer 2006, Pyšek and Richardson 2007, Blackburn and Jeschke 2009, Schlaepfer *et al*. 2010, van Kleunen *et al*. 2010). In this context, species invasiveness is a plant trait that can be related to other plant traits (e.g. Hamilton *et al*. 2005). Building on these discussions, I suggest that the use of a complementary CS and PIC approach can allow invasion ecologists to harness a powerful tool for understanding the evolutionary nature of life-history trait relationships with species invasiveness. Consistent patterns of correlated trait divergences across multiple, independent phylogenetic radiations provide strong evidence for traits that have evolved as key drivers of invasion success on many occasions. Detecting such consistent trait patterns has the potential to lead us to a deeper understanding of how some species are able to become widespread and persistent invaders of ecosystems (Rejmánek and Pitcairn 2002, Pimentel *et al.* 2005, Simberloff 2005), while the greater proportion of an exotic flora does not become invasive (Jeschke and Strayer 2005).

A small number of studies have specifically incorporated phylogenetic information to compare invasive species with native species, with the view to determine why the invasive species are able to out-compete the native flora (Blaney and Kotanen 2001, Cadotte and Lovett-Doust 2001, Vilà and Weiner 2004, Bossdorf *et al*. 2005, Mason *et al*. 2008, Dostál 2011). For example, Blaney and Kotanen (2001) used seeds of paired congeneric native and invasive species to determine whether a lowered rate of fungal pathogenic attack on seeds promoted invasiveness within two regions (wetland and upland) of the introduced range. They found the effects of a fungicide treatment on the survival of buried seeds did not differ overall between native species and exotic species, although the seeds of the exotic species were recovered at a higher rate than seeds of natives in uplands, but this effect was not attributable to fungal pathogens. In another example, Dostál (2011) examined competitive interactions within 12 triplets, each consisting of an invasive species, a native congeneric (or confamilial) species, and a native heterogeneric species. The study tested experimentally whether invasiveness of exotic species may be due to nonequivalent competitive interactions between native and invasive species. The competitive interactions occurring between the species triplets, including overlaps in resource use, improved competitiveness, and production of novel allelochemicals were found to be statistically equivalent and therefore did not account for invasiveness within the study species.

The ‘native-comparison’ approach (sensu Hamilton *et al*. 2005) compares the life-history traits of native with non-native species in the new environment (Crawley *et al*. 1996, Cadotte and Lovett-Doust 2001, Lake and Leishman 2004). This approach answers the question, what traits of the invading species enhance their potential to increase in abundance over native species? This approach therefore provides very different information to the question at the heart of the present study: what traits distinguish successful invaders from non-native species that have not invaded successfully? One issue with the native-comparison approach is that among a pool of species native to a study region, some native species will also have become invasive because of changes in land-use brought about by human activities. Thus, it is crucial that these species are accounted for in any comparisons between native and non-native species (e.g. Leishman and Thomson 2005). A further issue with the native-comparison approach in an evolutionary framework is that the number of independent evolutionary divergences that can be compared for shifts in life history between natives and exotics is often limited. In the present thesis, a key goal is to explore the use of the complementary CS and PIC approach in understanding species invasiveness. Given the limited opportunities to do this with native-comparison approach, it is not considered further here.

The work presented in this thesis adopts a 'target-area' approach. A target-area approach focuses on the pool of exotic plant species that have already established in a region and relates life-history trait variation to species invasiveness (Pyšek *et al*. 1995, Rejmánek and Richardson 1996, Grotkopp *et al*. 2002, Brändle *et al*. 2003, Lloret *et al*. 2004, Hamilton *et al*. 2005). Three approaches have been adopted in previous studies that have used a target-area approach to examine trait relationships with species invasiveness. Some studies have not explicitly considered phylogeny in trait analyses (the CS approach only), some have only used a PIC approach (in most cases the reasoning is that the PIC approach is statistically more 'valid') and a small number have used a complementary approach (both CS and PIC analyses). In general, most studies have to this time used CS analyses only. The relative paucity of studies using both CS and PIC analyses is probably a result of the ideas established in other areas of plant ecology not 'migrating' to invasion ecology. Given this situation, I describe in the following section a range of important issues that must be considered in the appropriate selection of species for using the complementary CS and PIC approach in studies relating species invasiveness to plant life history. My aim is to provide a generalized framework that can be used by invasion ecologists the world over regardless of the geographic region, taxa studied or the 'type' of invasiveness examined.

3.2.4 CRITERIA FOR SPECIES SELECTION

In this section, I describe why it is important to ensure rigorous selection criteria are employed when selecting species for comparison in complementary CS-PIC analyses. Here, I present a series of important considerations that make up an operating framework for comparative studies of species invasiveness. The selection criteria underpinning the framework can be implemented to provide the most meaningful comparisons between invasive and non-invasive species groups.

3.2.4.1 CONSISTENCY IN THE DEFINITION OF INVASIVENESS

It is important to have a consistent definition of species invasiveness when performing comparative analyses. Spatial scale is an important factor in determining invasiveness (Sax and Gaines 2003, Herben *et al*. 2004, Cadotte and Fukami 2005). A locally 'invasive' species may be defined in a markedly different way to a species considered invasive on a regional or continental scale. For instance, locally-invasive species are often measured using continuous scales including local abundance and percentage canopy cover within a given area, whereas species considered invasive on a continental scale are often measured using area of continental occupancy, number of habitats invaded and rate of geographic spread. Although prolific plant spread on either scale qualifies a plant species as invasive within context, selecting species for ecologically comparative purposes using inconsistent definitions of invasiveness may reduce the relevance and meaningfulness of the study findings. If the definition of invasiveness in a given study is an exotic species which has a high local abundance, in order to create a sound ecological comparison the non-invasive contrast must be an exotic species which maintains a low local abundance, not an exotic species considered non-invasive due to having a narrow geographic distribution. Likewise, if invasiveness is measured as an exotic species having a wide geographic distribution within the introduced range, then this should be contrasted with a species which has a comparatively narrow geographic distribution, as opposed to an exotic species considered non-invasive due to having a low environmental impact.

3.2.4.2 PHYLOGENETICALLY-INDEPENDENT CONTRASTS

A key strength of using PIC analysis is that it can be used to unravel the evolutionary nature of trait relationships across a phylogeny (Felsenstein 1985). Given that invasiveness can be linked with taxonomic patterns (Daehler 1998, Pyšek 1998, van Kleunen *et al*. 2007, Pyšek et al. 2008), PIC analyses exploring the evolutionary underpinnings of trait associations with invasiveness can unravel whether the trait has diverged multiple times across a phylogeny or if it is attributed to a single node higher up within a phylogeny. Using single PIC pairs from multiple different genera prevents bias which could occur if a PIC pair from a single genus is compared with five PIC pairs from only one other genus. Using multiple congeneric contrasts of invasiveness across a wide taxonomic profile allows us to observe whether the correlated divergences in invasiveness associated with the divergence in a species trait form a consistent pattern across the phylogeny.

3.2.4.3 RESIDENCE TIME IN THE INTRODUCED RANGE

Recent studies have demonstrated that residence time (i.e. the time that an exotic species has been present in the introduced range) is linked to invasiveness (Hobbs and Humphries 1995, Daehler 2009, Phillips *et al*. 2010a). As species typically experience a lag before population increase during the initial establishment phase of the invasion pathway, and certainly given that most exotic species introductions to new regions typically begin with only a few individuals, it follows logically that the longer an exotic species resides in a new range, the more opportunity it will have to accumulate necessary resources, reproduce, expand in abundance and potentially become invasive. Thus, when establishing a set of invasive vs. non-invasive contrasts, it must be ensured that the paired species have a similar residence time. Otherwise, spurious correlations may emerge for particular traits to be correlated with invasiveness, when in fact such traits are actually correlated with residence time. Such traits are in fact secondary correlates of invasiveness after the effects of long residence time in driving invasiveness.

Given that different plant growth forms have different lag times prior to becoming invasive, growth-form appropriate residence times must be considered.

Approximate lag times after which different growth forms express invasiveness following introduction have been reported for grasses as ≥ 60 years, shrubs ≥ 55 years, trees ≥ 80 years and vines ≥ 40 years (Daehler 2009). Such lag times can be used in the construction of a comparative dataset to ensure that non-invasive species are truly non-invasive and not likely to be impeded by an allee effect, whereby a species' overall fitness is reduced when population densities are low, an abundance-related effect which occurs naturally in the early stages of colonisation (Allee 1931, Taylor and Hastings 2005).

3.2.4.4 HABITAT CO-OCCURRENCE

Exotic species that form self-sustaining populations in the introduced range are often exposed to an extraordinarily diverse range of environmental characteristics, including resource opportunities and limitations, which can positively or negatively influence the invasion success of exotic species. The survival, growth and reproduction of plant species are readily affected by habitat conditions including temperature and rainfall fluctuations, soil conditions, nutrient loads, and the presence or absence of other resource competitors, mutualists, herbivores and pathogenic species. It has been shown that habitat-related and community-related biases can be effectively minimized if the closely-related species used within a comparative study co-occur within the same habitats (Skálová *et al*. 2012). It is therefore important to account for the environmental co-occurrence of the exotic species pair when performing a species comparison.

3.2.4.5 GROWTH FORM

There are equivocal findings in the literature for the role of plant growth form in invasiveness. In some cases, studies report no significant tendency for particular growth forms to be more invasive than others. On the other hand, research has indicated that some growth forms are more likely to be over-represented among invasives (e.g. long-lived, monoecious trees, Sutherland 2004). While a particular growth form may be important for invasiveness in one part of the world, a different growth form might be more dominant in other pools of invasive species in other parts of the world (e.g. Crawley *et al*. 1996, Williamson and Fitter 1996a). In Chapter 2, I identified that growth form was significantly related to invasiveness in the naturalised flora of Australia, with climbers significantly more likely to become invasive compared to trees. In situations where growth form is known to be correlated with invasiveness, perhaps underpinned by longer life span in one growth form versus another (Sutherland 2004), it is important to control for growth form when establishing phylogenetic contrasts. This prevents spurious correlative patterns from entering into potential explanations for invasiveness. For instance, small seed size is a trait that has been linked to invasiveness (e.g. Hamilton *et al*. 2005). But small seed size is also more likely to be associated with particular growth forms (e.g. grasses and forbs, Salisbury 1942, Baker 1972, Foster and Jansen 1985, Leishman *et al.* 1995). A study that finds small seed size is linked with invasiveness, that hasn't controlled for growth form, cannot untangle growth-form related explanations for invasiveness from explanations related to seed size. In the worst case scenario, seed size might be touted as the driver of invasiveness but in fact growth traits are the direct link to invasiveness and seed size is simply a secondary correlate.

3.3.1 AN EMPIRICAL TEST OF THE FRAMEWORK

I used the selection criteria described above to examine relationships between species invasiveness and life-history traits in naturalised exotic plant species in Australia. I employed a complementary approach involving CS and PIC methods of analysis. My aims were to (i) identify cross-species correlations between invasiveness and life-history traits and (ii) determine whether evolutionary divergences in invasiveness (i.e. divergences between invasive and non-invasive species) have been consistently correlated with evolutionary divergences in life-history traits. This is a desktop study utilizing a wide range of botanical sources to extract life-history information on the naturalised exotic flora introduced to Australia.

Specifically, I tested the following four predictions:

(i) *Invasive species have smaller seed mass than non-invasive species.*

There is a wealth of empirical evidence for the interspecific trade-off between seed mass and seed output (Werner and Platt 1976, Shipley and Dion 1992, Westoby *et al.* 1992, Greene and Johnson 1994, Turnbull *et al.* 1999, Jakobsson and Eriksson 2000, Leishman *et al.* 2000, Henery and Westoby 2001). For a given investment of plant resources in seed production, species can produce either many small seeds or few large seeds (or somewhere in between) per reproductive event (Smith and Fretwell 1974, Leishman *et al.* 2000, Westoby *et al.* 2002). It has been postulated that prolific seed production – and hence small seed size based on the well-documented size-number trade-off – is an important contributor to invasion success in plants (Hamilton *et al.* 2005). For the naturalised exotic flora in Australia, I predicted that small seed mass would be correlated with invasiveness in CS analysis if prolific seed production linked to small seed size is a driver of invasiveness. If this is the case, then the emergence of a significant relationship between seed mass and invasiveness in a complementary independent-contrasts analysis will indicate that the relationship has evolved independently on multiple occasions. In contrast, the lack of significant relationship in a PIC analysis will indicate that the relationship has evolved on one (or at most a few) occasions deep in the phylogeny.

(ii) *Invasive species have larger leaves than non-invasive species.*
Large leaf size is a plant growth trait that is often associated with invasiveness (Reich *et al.* 1997). Comparatively larger leaves provide increased photosynthetic capacity and faster relative growth rate, thus providing an invasive advantage when colonising new habitats (Grotkopp *et al.* 2002, Lake and Leishman 2004, Leishman and Thomson 2005). For the naturalised exotic flora found in Australia, I predict that large leaf size will be correlated with invasiveness in CS analysis if increased photosynthetic capacity and faster relative growth rate via leaf size are drivers of invasiveness. If this is the case, then the emergence of a significant relationship between leaf size and invasiveness in a complementary PIC analysis will indicate that the relationship has evolved independently on multiple occasions. In contrast, the lack of a significant PIC relationship will indicate that the relationship has evolved on one (or at most a few) occasions deep in the phylogeny.

(iii) *Invasive species are capable of attaining greater canopy height than non-invasive species.*
Typical maximum canopy height of adult plants represents a species' ability to compete for light (Weiher *et al.* 1999, Westoby *et al.* 2002, Falster and Westoby 2003). Previous work has shown that exotic plant species have higher maximum height than co-occurring native plant species (Williamson and Fitter 1996a, Crawley *et al.* 1996,

Ordonez *et al.* 2010). Higher maximum height can also distinguish invasive from non-invasive exotic plant species (Goodwin et al. 1999, but see Hamilton *et al.* 2005, Lloret *et al.* 2005, Cadotte *et al.* 2006). For the naturalised exotic flora in Australia, I predict that increased maximum height will be correlated with invasiveness in CS analysis if ability to compete for light via height gain is a driver of invasiveness. If this is the case, then the emergence of a significant relationship between maximum height and invasiveness in a complementary PIC analysis will indicate that the relationship has evolved independently on multiple occasions. In contrast, the lack of a significant PIC relationship will indicate that the relationship has evolved on one (or at most a few) occasions deep in the phylogeny.

(iv) *Invasive species use a larger number of propagule dispersal mechanisms than non-invasive species.*

As propagule dispersal distances from source populations increase, so does the likelihood of an exotic plant species establishing new populations across a broader geographic range (Bawa and Hadley 1990). Several studies have shown invasive species spreading across greater distances through the use of multiple propagule dispersal mechanisms (Carlton 1993, Hampe 2004, Saumel and Kowarik 2009). For the naturalised exotic flora in Australia, I predict that the ability to use a larger number of propagule dispersal mechanisms will be correlated with invasiveness in CS analysis if increased dispersal distance of propagules via multiple dispersal mechanisms is a driver of invasiveness. If this is the case, then the emergence of a significant relationship between the number of propagule dispersal mechanisms and invasiveness in a complementary PIC analysis will indicate that the relationship has evolved independently on multiple occasions. In contrast, the lack of a significant PIC relationship will indicate that the relationship has evolved on one (or at most a few) occasions deep in the phylogeny.

In addition to predictions for these four plant traits, I examine relationships between invasiveness and individual dispersal mechanisms including water dispersal, wind dispersal, adhesive dispersal (physical attachment to another moving source) and dispersal by animal consumption (i.e. ‘endozoochory’) to determine whether there is evidence for differential use of these dispersal mechanisms between invasive and non-invasive species. My working hypothesis for each of these dispersal traits is that invasive species are more likely than contrasted non-invasive species to possess mechanisms that assist in the dispersal of propagules to new regions.

3.3.2 MATERIALS AND METHODS

3.3.2.1 STUDY SPECIES AND DATASET COMPILATION

I compiled a dataset of congeneric pairings of an invasive with a non-invasive species from the pool of naturalised exotic plant species introduced to Australia since the beginnings of permanent European settlement in 1770 (Table 3.1). To construct this dataset of congeneric contrasts, I began by first selecting all 132 species currently considered as invasive in Australia (category '5A' in Randall 2007; see also Murray and Phillips 2012). I matched each invasive species with all naturalised exotic congeners that have an ongoing non-invasive status within Australia (species listed with just the category 'N' in Randall 2007). A total of 52 invasive species did not have a non-invasive congener and were excluded from the dataset as the explicit focus of this study was on comparing closely-related species within the same genus. I also sought further evidence that non-invasive species selected thus far for the dataset have not spread invasively within Australia by performing web searches of the species' activity in Australia and assessing regional council weed lists for any reports of invasiveness. No evidence was found that these non-invasive species have been reported as invasive anywhere in Australia.

To ensure that non-invasive species were unequivocally restricted in their geographic range and invasive species were widespread at a continental scale, I undertook the following procedure. I determined geographic range sizes of the invasive and non-invasive species as area of occupancy (see Hamilton *et al*. 2005) across Australia using data obtained from herbarium records maintained at Australia's Virtual Herbarium (http://avh.rbg.vic.gov.au/avh/; accessed July 2010). Within each congeneric contrast, I only selected non-invasive species with a current area of occupancy within Australia of less than 12 km^2. In addition, the continental range sizes of the invasive species in each contrast had to measure approximately ten times larger than the ranges of non-invasive congeners. This procedure resulted in the exclusion of 27 invasive species as no legitimate contrasts could be established with these species for the purposes of this study.

Table 3.1. Congeneric contrasts established for the study following the species selection process. MRT represents a species' minimum residence time within Australia. MAO represents the minimum area of continental occupancy of the species within Australia. The symbol (*) indicates that the species precise native range is obscure.

Species	Family	Invasive	Growth form	MRT (years)	MAO(km^2)	Native range
Ageratina adenophora	*Asteraceae*	Yes	Herb	137	170	N. America
Ageratina ligustrina	*Asteraceae*	No	Shrub	103	3	N. America, S. America
Allium vineale	*Alliaceae*	Yes	Herb	156	57	Europe, Asia, Africa
Allium paniculatum	*Alliaceae*	No	Herb	97	5	S. Europe, Asia, N. Africa
Andropogon virginicus	*Poaceae*	Yes	Herb	67	96	N. America, S. America
Andropogon distachyos	*Poaceae*	No	Herb	76	1	Europe
Annona glabra	*Annonaceae*	Yes	Tree	166	71	W. Africa, N. America, S. America
Annona reticulata	*Annonaceae*	No	Tree	192	8	N. America
Aristolochia elegans	*Aristolochiaceae*	Yes	Vine	112	92	S. America (Argentina, Bolivia, Brazil)
Aristolochia grandiflora	*Aristolochiaceae*	No	Vine	124	1	Caribbean (Jamaica)
Asparagus asparagoides	*Liliaceae*	Yes	Shrub	166	159	S. Africa
Asparagus falcatus	*Liliaceae*	No	Shrub	121	3	Central and S. Africa, Asia
Bryophyllum delagoense	*Crassulaceae*	Yes	Herb	31	126	Africa
Bryophyllum proliferum	*Crassulaceae*	No	Shrub	137	9	Africa

Chloris gayana	*Poaceae*	Yes	Herb	109	396	Africa (*)
Chloris ciliata	*Poaceae*	No	Herb	78	1	N. America, S. America, Caribbean Islands
Coreopsis lanceolata	*Asteraceae*	Yes	Herb	149	159	N. America
Coreopsis grandiflora	*Asteraceae*	No	Herb	59	8	N. America
Ehrharta longiflora	*Poaceae*	Yes	Herb	131	468	S. Africa
Ehrharta brevifolia	*Poaceae*	No	Herb	131	4	S. Africa
Eragrostis curvula	*Poaceae*	Yes	Herb	91	594	Africa
Eragrostis superba	*Poaceae*	No	Herb	130	4	Africa
Erica lusitanica	*Ericaceae*	Yes	Shrub	131	179	Europe (France, Spain, Portugal)
Erica caffra	*Ericaceae*	No	Tree	123	9	S. Africa
Genista monspessulana	*Leguminosae*	Yes	Shrub	151	466	Africa, Asia, Europe
Genista tinctoria	*Leguminosae*	No	Shrub	158	5	Asia, Europe
Ipomoea cairica	*Convolvulaceae*	Yes	Climber	166	237	Africa, Asia (*)
Ipomoea pandurata	*Convolvulaceae*	No	Climber	112	3	North America
Juncus articulatus	*Juncaceae*	Yes	Herb	105	816	Europe, Asia, Africa, N. America
Juncus inflexus	*Juncaceae*	No	Herb	69	11	Europe (Mediterranean), Asia, Africa
Ligustrum sinense	*Oleaceae*	Yes	Shrub	148	187	Asia (China, Hong Kong, Taiwan, Vietnam)
Ligustrum ovalifolium	*Oleaceae*	No	Shrub	144	2	Asia (Japan, S. Korea)
Lonicera japonica	*Caprifoliaceae*	Yes	Shrub	192	149	Asia (E. China, Japan, Taiwan)
Lonicera fragrantissima	*Caprifoliaceae*	No	Shrub	107	10	Asia (E. China)

Lycium ferocissimum	*Solanaceae*	Yes	Shrub	164	607	S. Africa
Lycium afrum	*Solanaceae*	No	Shrub	124	6	S. Africa
Nassella neesiana	*Poaceae*	Yes	Herb	75	154	S. America
Nassella megapotamia	*Poaceae*	No	Herb	64	6	S. America
Opuntia imbricata	*Cactaceae*	Yes	Shrub	158	74	N. America
Opuntia dejecta	*Cactaceae*	No	Shrub	137	1	N. America
Paspalum dilatatum	*Poaceae*	Yes	Herb	133	428	S. America
Paspalum dasypleurum	*Poaceae*	No	Herb	79	5	S. America
Passiflora foetida	*Passifloraceae*	Yes	Vine	166	672	S. America (Ecuador)
Passiflora coccinea	*Passifloraceae*	No	Vine	166	2	S. America (Bolivia)
Salvia coccinea	*Lamiaceae*	Yes	Herb	158	158	N. America, S. America
Salvia splendens	*Lamiaceae*	No	Herb	166	2	S. America (Brazil)
Solanum torvum	*Solanaceae*	Yes	Tree	95	252	Asia (China), N. America, S. America
Solanum betaceum	*Solanaceae*	No	Tree	126	9	S. America
Tamarix aphylla	*Tamaricaceae*	Yes	Tree	73	94	Africa, Asia
Tamarix gallica	*Tamaricaceae*	No	Tree	145	2	Africa (Canary Islands)
Tecoma capensis	*Bignoniaceae*	Yes	Shrub	192	30	Africa
Tecoma alata	*Bignoniaceae*	No	Shrub	124	2	S. America (Peru)
Tradescantia fluminensis	*Commelinaceae*	Yes	Herb	138	99	S. America
Tradescantia spathacea	*Commelinaceae*	No	Herb	154	9	N. America, S. America

Table 3.2. Life-history traits of the congeneric contrasts of plant invasiveness.. Seed mass data were available for 16 of the 27 contrasts.

Species	Family	Invasive	Seed mass (mg)	Leaf size (mm^2)	Maximum height (cm)
Ageratina adenophora	*Asteraceae*	Yes	0.0677	7560	200
Ageratina ligustrina	*Asteraceae*	No	0.0100	4725	500
Allium vineale	*Alliaceae*	Yes	0.0190	2520	75
Allium paniculatum	*Alliaceae*	No	0.0013	1750	80
Andropogon virginicus	*Poaceae*	Yes	0.0003	2135	100
Andropogon distachyos	*Poaceae*	No	0.0009	700	100
Annona glabra	*Annonaceae*	Yes	0.1248	5880	1000
Annona reticulata	*Annonaceae*	No	0.2392	7000	1000
Aristolochia elegans	*Aristolochiaceae*	Yes	0.0021	15400	600
Aristolochia grandiflora	*Aristolochiaceae*	No	0.0299	14000	800
Asparagus asparagoides	*Liliaceae*	Yes	0.0082	315	300
Asparagus falcatus	*Liliaceae*	No	0.0384	437.5	700
Bryophyllum delagoense	*Crassulaceae*	Yes	-	525	180
Bryophyllum proliferum	*Crassulaceae*	No	-	5250	150
Chloris gayana	*Poaceae*	Yes	-	840	120
Chloris ciliata	*Poaceae*	No	-	126	100

Coreopsis lanceolata	*Asteraceae*	Yes	0.0027	4200	100
Coreopsis grandiflora	*Asteraceae*	No	0.0023	1155	60
Ehrharta longiflora	*Poaceae*	Yes	-	1260	90
Ehrharta brevifolia	*Poaceae*	No	-	560	40
Eragrostis curvula	*Poaceae*	Yes	0.0720	1750	100
Eragrostis superba	*Poaceae*	No	0.7000	2800	120
Erica lusitanica	*Ericaceae*	Yes	0.1150	4.9	300
Erica caffra	*Ericaceae*	No	0.0140	66.5	450
Genista monspessulana	*Leguminosae*	Yes	0.0086	140	300
Genista tinctoria	*Leguminosae*	No	0.0081	157.5	90
Ipomoea cairica	*Convolvulaceae*	Yes	-	5670	500
Ipomoea pandurata	*Convolvulaceae*	No	-	11550	350
Juncus articulatus	*Juncaceae*	Yes	0.0200	140	80
Juncus inflexus	*Juncaceae*	No	0.0300	1680	120
Ligustrum sinense	*Oleaceae*	Yes	-	875	500
Ligustrum ovalifolium	*Oleaceae*	No	-	851.2	350
Lonicera japonica	*Caprifoliaceae*	Yes	0.0033	2240	900
Lonicera fragrantissima	*Caprifoliaceae*	No	0.0027	560	250
Lycium ferocissimum	*Solanaceae*	Yes	-	280	400
Lycium afrum	*Solanaceae*	No	-	63	200

Nassella neesiana	*Poaceae*	Yes	0.0071	3500	120
Nassella megapotamia	*Poaceae*	No	0.0024	5880	130
Opuntia imbricata	*Cactaceae*	Yes	-	-	300
Opuntia dejecta	*Cactaceae*	No	-	-	200
Paspalum dilatatum	*Poaceae*	Yes	-	3780	200
Paspalum dasypleurum	*Poaceae*	No	-	1400	80
Passiflora foetida	*Passifloraceae*	Yes	0.0083	3430	500
Passiflora coccinea	*Passifloraceae*	No	0.0078	13512.8	350
Salvia coccinea	*Lamiaceae*	Yes	0.0021	1225	100
Salvia splendens	*Lamiaceae*	No	0.0044	1400	120
Solanum torvum	*Solanaceae*	Yes	0.0094	28980	500
Solanum betaceum	*Solanaceae*	No	0.0048	73500	500
Tamarix aphylla	*Tamaricaceae*	Yes	0.7975	1750	1300
Tamarix gallica	*Tamaricaceae*	No	0.0100	11.2	800
Tecoma capensis	*Bignoniaceae*	Yes	-	700	300
Tecoma alata	*Bignoniaceae*	No	-	1050	300
Tradescantia fluminensis	*Commelinaceae*	Yes	-	962.5	50
Tradescantia spathacea	*Commelinaceae*	No	-	1102.5	38

Non-invasive species with current residence times within Australia that had not surpassed expected lag phases for invasiveness were removed from consideration at this point. Based on recent estimates from Daehler (2009), non-invasive grasses with residence times <60 years, shrubs with residence times <55 years, trees with residence times <80 years, and vines with residence times <40 years were removed. Species pairs were also chosen by having naturalised populations of both species co-occurring within a common IBRA bioregion.

The IBRA (Interim Biogeographic Regionalisation for Australia) region system was created as a landscape based approach to classifying the land surface of Australia. From this initiative, 85 unique bioregions were identified across the landscape of Australia. Bioregions are distinct geographic units, each reflecting a unifying set of major environmental influences which shape the occurrence of flora and fauna and their interaction with the physical environment (Thackway and Cresswell 1995). For this reason I consider IBRA regions to be an effective continental-scale measure to ensure equitability in the comparison of species. In cases where this still left multiple non-invasive species for comparison with an invasive congener, where possible, non-invasive species were selected with (i) the closest residence time matching the invasive species, (ii) the same native range as the contrasted invasive species and (iii) the same growth form as the contrasted invasive congener. These final species selection criteria led to the formation of the final dataset totalling 54 species, comprised of 27 congeneric pairings of an invasive with a non-invasive species, spanning 21 taxonomic families (Table 3.1).

Direct information on colonization and propagule pressure was not available for the bulk of Australia's introduced flora because of the immense number of transportation vectors and the limited records available from early colonial quarantines, importation manifests and commercial wholesalers. Instead, I used residence time as 'proxy' of propagule pressure. Residence time integrates a suite of factors that can influence invasiveness, including the likelihood of an exotic species becoming naturalised, occupying a large geographic range, and overcoming a lag phase (Richardson and Pyšek 2006).

3.3.2.2 PLANT LIFE-HISTORY TRAITS

Plant trait data on total number (and type) of propagule dispersal mechanisms, seed mass, leaf size and maximum canopy height were gathered using a range of both published and unpublished sources, including national and regional floras, herbarium records and the Census of Cultivated Plants database (Table 3.2seed). Data on seed mass were standardized in metric units (g). Leaf size was calculated using maximum leaf length and leaf width measurements. I used the equation leaf size = length x width x 0.7 (Kraft *et al.* 2008). This equation has been shown to estimate leaf size reliably for 742 Neotropical species and has subsequently been used to estimate the leaf size of 231 tree and shrub species from Australian subtropical rainforests (Kooyman *et al.* 2010) and the leaf size of 270 Australian tropical and temperate climbers (Gallagher *et al.* 2011). Data on maximum plant height was standardized in metric units (cm). The highest recorded plant canopy height value was selected to reflect the maximum known potential for vertical growth in each species.

I also collected information on the number and type of mechanisms each species uses for propagule dispersal, and included all evidence of dispersal beyond the specific morphological properties of the propagule. I define propagule here as all parts of a seed and attached appendages (i.e. wings, burrs, fruit flesh). Dispersal mechanisms included wind dispersal, water dispersal, adhesive dispersal (physical attachment to another moving source) and endozoochory (dispersal via consumption and seed deposition by animals). I totalled the number of propagule dispersal mechanisms recorded for each species. Species with no records of using any of these dispersal mechanisms for their propagules had their propagule dispersal listed as ‘unassisted’ (e.g. Murray *et al*. 2002).

3.3.2.3 STATISTICAL ANALYSIS

Two analytical approaches were used to quantify relationships between species invasiveness and life-history traits. In the CS analysis, trait relationships were explored with no explicit consideration of phylogenetic relationships among species. A PIC analysis was then performed to explore evolutionary-divergence correlations between species invasiveness and plant life-history traits.

Cross-species relationships between invasiveness and life-history traits

Cross-species variation in life-history traits (explanatory variables) was related to species invasiveness (response variable) using generalized linear models. Since the response variable was categorical with two levels (invasive, non-invasive), I modelled relationships using a binomial probability distribution and a Logit link function (Crawley 2007). I used Bonferroni corrections to correct for potential type I errors which can occur with multiple tests of the same dataset (Gotelli and Ellison 2004). After Bonferroni correction, the critical P value for significance was 0.00625. All analyses were performed using SPSS v. 19.0 (SPSS Chicago, IL, USA).

Phylogenetically-independent-contrasts analysis

All PIC analyses were performed using the open-source statistical program "R" (R Development Core Team 2007). The first step in the PIC analysis was to construct a phylogenetic tree representing the evolutionary relationships among the study species. I used PHYLOMATIC v. 4.1 (Webb and Donoghue 2005) to construct the phylogenetic tree which was based on the APG3 derived megatree R20091110. This tree is a strict consensus phylogeny for angiosperm plants which uses a complete resolution as determined by the Angiosperm Phylogeny Group (Stevens 2009). The nodes of the phylogeny were then dated using times established by Wikström *et al*. (2001) and attached to the phylogeny using the PHYLOCOM BLADJ package (Webb *et al.* 2008; see Fig. 3.1).

I tested whether the study phylogeny required transformation to binary format using the "is.binary.tree" command in APE. This is necessary because APE requires phylogenetic trees to be in binary format as opposed to multichotomous (i.e. multiple splits from a single node) format. The test result indicated the tree was not in binary format; therefore I transformed the phylogenetic tree structure from multichotomous to dichotomous (binary) format using the "multi2di" function in APE. I then performed a series of phylogenetic logistic regressions for each life-history trait in relation to invasiveness using the "pic" function in APE. In each regression, invasiveness was used as a binary response variable, and each life-history trait was an explanatory variable. In the case of analysing seed mass and leaf size, separate phylogenetic trees were created using the process described above for the 16 PICs which had available seed mass data and the 26 PICs with leaf size data (a PIC pair representing the genus Opuntia was excluded due to being succulent plants without typical leaf morphology), as APE requires a complete trait dataset when performing phylogenetic comparisons in R.

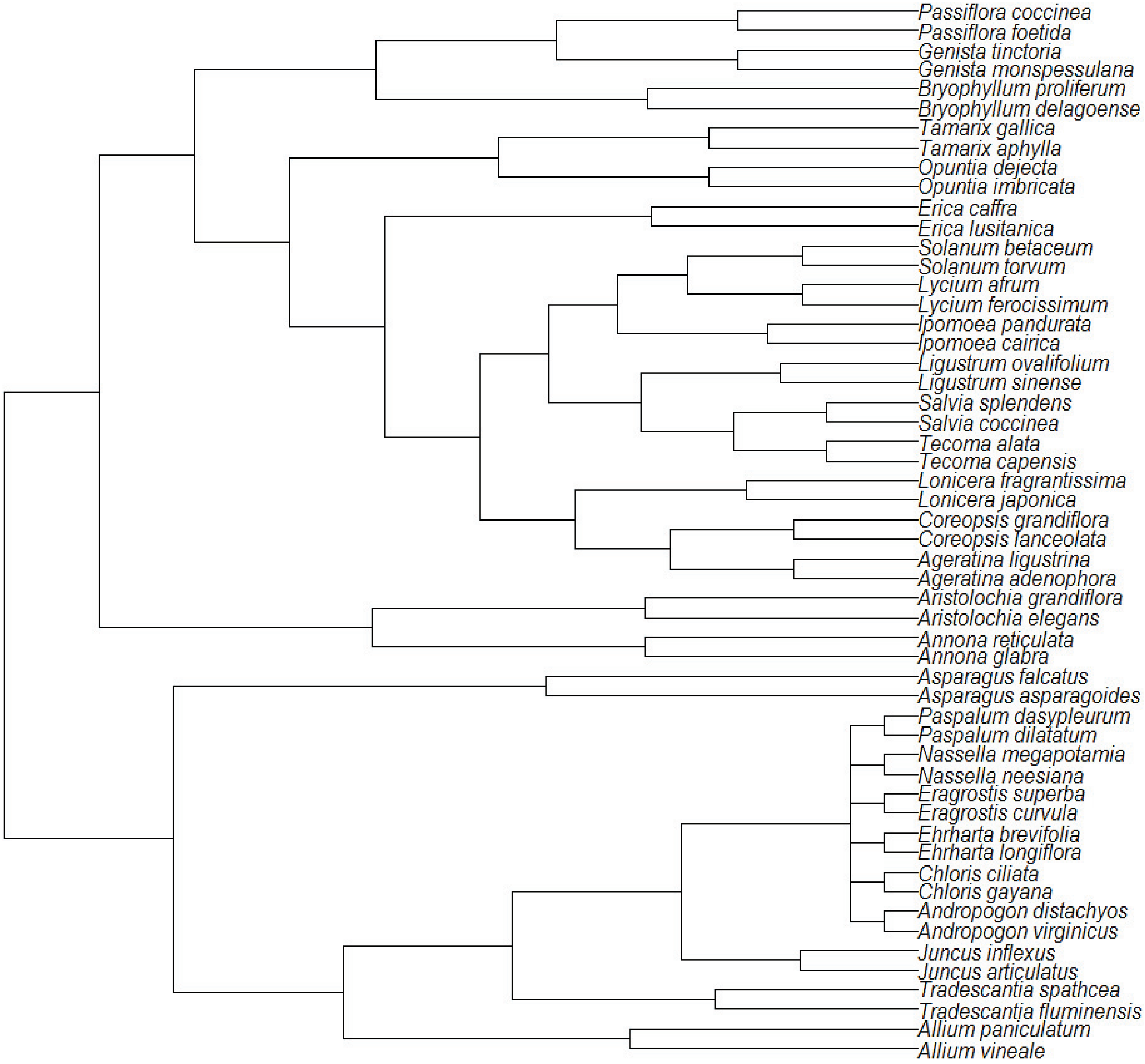


Figure 3.1.

Phylogenetic tree of the study species. Internal nodes were dated based on clade age estimates provided by Wikström *et al.* (2001).

3.4 RESULTS

3.4.1 CROSS-SPECIES ANALYSES

3.4.1.1 Seed mass

There was no significant relationship between species invasiveness and seed mass ($F_{1,32}$ = 0.023, P = 0.880; Fig. 3.2a). This result does not support the prediction that seeds of invasive species are comparatively smaller than those of non-invasive species.

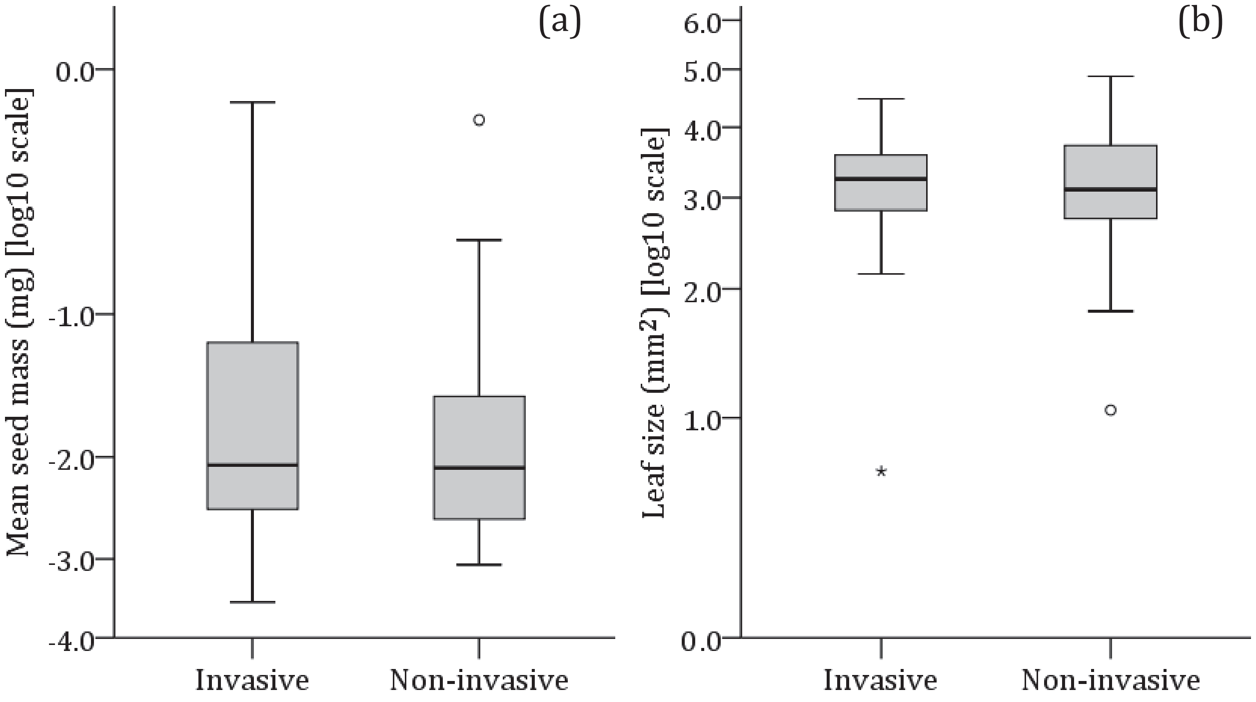


Figure 3.2. Box plots comparing a) seed mass and b) leaf size between invasive and non-invasive species. The box plots reveal the distribution and skew of the life-history trait data, from the smallest observation (i.e. lower error bar) to the largest observation (i.e. upper error bar). The data median is indicated as the line within the grey box. Data outliers are represented by the symbols ° and *.

3.3.1.2 Leaf size

Leaf size was found not to differ significantly between invasive and non-invasive species ($F_{1,52}$ = 0.476, P = 0.493; Fig. 3.2b). This result does not support the prediction that leaves of invasive species are larger than those of non-invasive species.

3.4.1.3 Maximum canopy height

Maximum canopy height was also found not to differ significantly between invasive and non-invasive species ($F_{1,54} = 0.456$, $P = 0.503$; Fig. 3.3). This finding does not support the prediction that invasive plant species have higher maximum canopy height compared to non-invasive species.

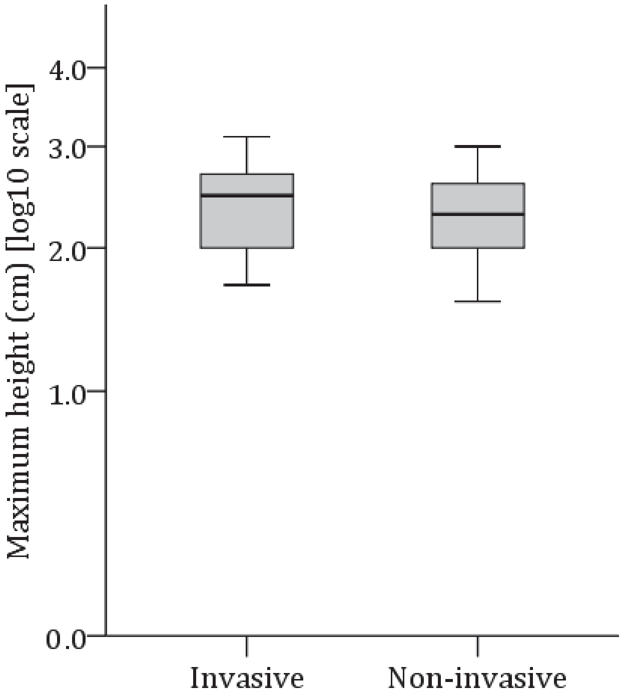


Figure 3.3. Box plots comparing maximum canopy height between invasive and non-invasive species.

3.4.1.4 Number of dispersal mechanisms

Species invasiveness was significantly related to number of propagule dispersal mechanisms with invasive plant species more likely to spread their propagules using a larger number of dispersal mechanisms compared to non-invasive species ($F_{1,54} = 10.618$, $P = 0.002$; Fig 3.4). Notably, invasive species were found to be more than twice as likely to use two dispersal mechanisms compared to non-invasive species and more than three times as likely to use three dispersal mechanisms (Fig 3.4). In one instance, the invasive species *Eragrostis curvula* was found to be capable of using all four defined dispersal mechanisms.

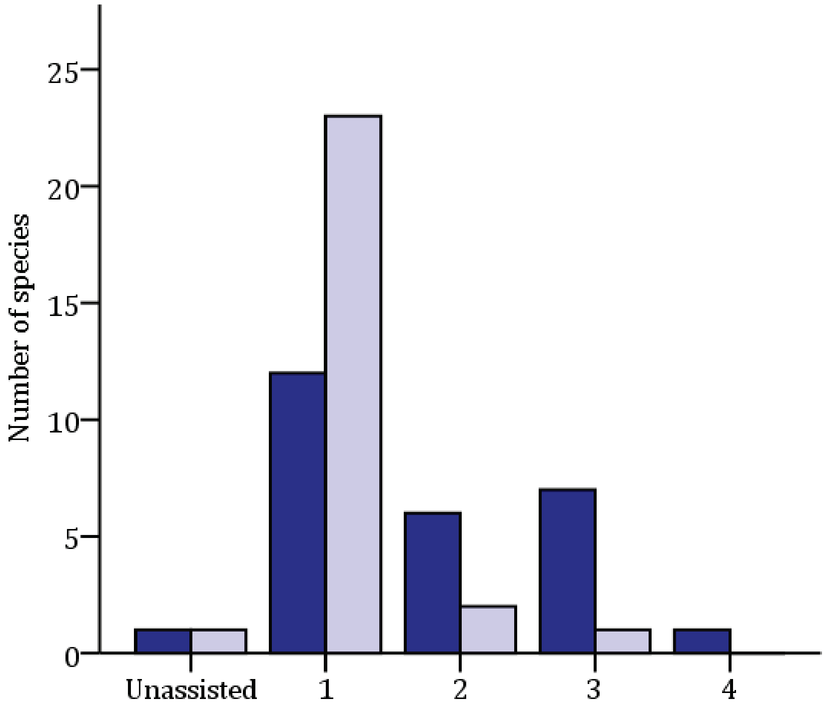


Figure 3.4. The number of invasive (dark blue bars) and non-invasive species (light blue bars) as a function of the total number of propagule dispersal mechanisms used.

3.4.1.5 Type of dispersal mechanism

Invasive species were also significantly more likely than non-invasives to disperse their propagules using water as a vector ($F_{1,54}$ = 18.000 , P <0.001; Fig. 3.5c). I found no such significant relationship between species invasiveness and the use of wind dispersal ($F_{1,54}$ = 0.071, P = 0.790; Fig. 3.5d), endozoochory ($F_{1,54}$ = 0.297, P = 0.588; Fig. 3.5b) or adhesion ($F_{1,54}$ = 2.559, P = 0.116; Fig. 3.5a).

3.4.2 CORRELATED-DIVERGENCE ANALYSES

Evolutionary divergences in invasiveness were found to be significantly correlated with divergences in the use of multiple propagule dispersal mechanisms ($F_{1,54}$ = 15.150, P = <0.001). Considered together with the significant cross-species relationship for this

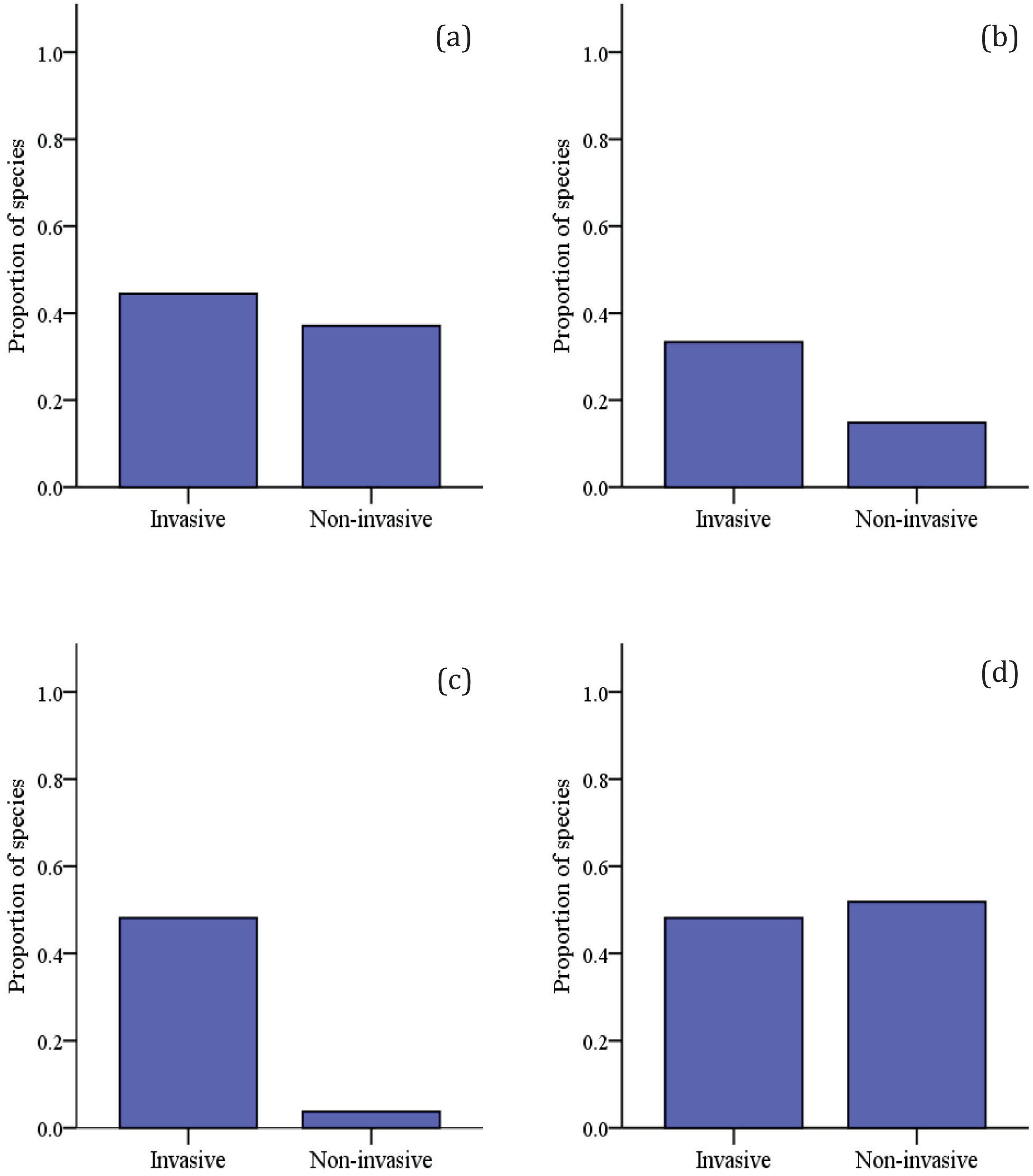


Figure 3.5. The proportions of invasive and non-invasive species that utilize each dispersal mechanism: (a) adhesion, (b) endozoochory, (c) water dispersal and (d) wind dispersal.

trait, this result indicates that there have been multiple independent evolutionary divergences between invasiveness and the use of multiple dispersal mechanisms across the study phylogeny. I also found that evolutionary divergences in invasiveness were correlated with divergences in the use of water dispersal of seeds ($F_{1,54}$ = 30.890, P = <0.001). The cross-species relationship between water dispersal and invasiveness is thus underpinned by multiple evolutionary divergences between invasiveness and water dispersal.

There were no significant evolutionary-divergence correlations between invasiveness and wind dispersal ($F_{1,54}$ = 0.199, P = 0.658), vertebrate adhesion ($F_{1,54}$ = 1.149, P = 0.289) and endozoochory ($F_{1,54}$ = 0.151, P = 0.699). Seed mass was also found not to be significantly related to invasiveness when phylogenetic relationships were considered ($F_{1,32}$ = 0.044, P = 0.835). Likewise, leaf size ($F_{1,52}$ = 0.046, P = 0.831) and maximum canopy height ($F_{1,54}$ = 0.049, P = 0.826) were found to have no evolutionary-divergence relationships with invasiveness.

3.5 DISCUSSION

I found that invasive species were significantly more likely to use a larger number of propagule dispersal mechanisms compared with non-invasive species in both CS and PIC analyses. This finding provides support for the idea that increased dispersal distance of propagules achieved through multiple dispersal mechanisms is an important driver of species invasiveness. A larger number of ways of dispersing propagules provides increased potential for invasion success by increasing the chances that the propagules will disperse to new locations away from the source population. My findings also indicate that the relationship between invasiveness and the use of multiple dispersal mechanisms has evolved on multiple, independent events across the phylogenetic tree describing my study species. Meeting the criteria of the conceptual framework I established has allowed the detection of very clear significant relationships between plant life-history and invasiveness and, importantly, the results of this study are not confounded with any of the issues covered in the selection criteria.

I also found that water dispersal of propagules was a significant correlate of invasiveness in both the CS and the PIC analyses. This finding demonstrates that the relationship between invasiveness and water dispersal has evolved on multiple, independent events across the phylogenetic tree describing my study species. Water dispersal of propagules is a dispersal mode that cannot be easily inferred from the shape or structures associated with propagules. Often, it is only the morphological adaptations of the propagule that are recognized by researchers when assessing the dispersal capabilities of a plant species. For instance, seeds encased in fleshy fruit, such as those produced by the invasive shrub *Lonicer*a *japonica,* commonly have their seed dispersal attributed solely to endozoochory (PCA-AWG report 2005, Ladwig and Meiners 2010). In fact, other research using dispersal observations and not just seed / fruit morphology has indicated that *L. japonica* seeds are also readily spread by water sources (Groves *et al*. 2005). This adds an entirely new dimension to the capacity for the species to spread across a landscape. Indeed, in many other cases, plant propagules are often dispersed in ways that cannot be inferred from morphological features of the propagule alone (Nathan and Muller-Landau 2000, Trakhtenbrot *et al*. 2005). The results of the present study indicate that it is important to ensure methods of plant dispersal which occur beyond the morphological properties of the propagule are accounted for when assessing the potential for invasive spread.

Dispersal of propagules by water has previously been found to enhance invasiveness in single-species studies. Hampe (2004) reported that seeds of invasive Glossy Buckthorn (*Frangula alnus*) that were initially dispersed by frugivorous birds into riparian habitats within the Aljibe Mountains, Europe (about 40 km NNW of Gibraltar) were spread further across the landscape by water flow dispersion. Interestingly, Carlton (1993) found that the combination of adhesion to the external panels of boats as well as water dispersal facilitated the spread of invasive zebra mussel (*Dreissena* spp.) to upstream sites in Lake Superior, Lake Michigan, and Lake Huron from founding populations in downstream Lake St. Clair (bordering northern USA and the province of Ontario, Canada). In these two case studies, the invasive species have been shown to use more than one dispersal mechanism – one of which was water – which facilitated further propagule spread across the landscape. In the case of the zebra mussel, water dispersal of propagules was enhanced by movement as a result of human activities (boating). Human-facilitated dispersal has often been associated with the accidental movement of plants to new regions (Baker 1986, Ruiz *et al.* 2000, Mortenson *et al.* 2009), and future study investigating human impacts on propagule dispersal of exotic plant species in Australia is certainly warranted.

Water dispersal of propagules has long been proposed as an important mechanism across an incredibly broad range of plant taxa (Darwin 1856). Flowing waterways such as rivers, streams and floodplains are important corridors for dispersal of the seed and vegetative propagules of plants (Merritt and Wohl 2002). Waterways often flow long distances in a single season via connected corridors and carry debris and organisms with very little friction (Vogt *et al.* 2004). Limited experimental work has been published on propagule dispersal in aquatic environments (Barrat-Segretain 1996, Andersson and Nilsson 2002, Boedeltje *et al.* 2003, Truscott *et al.* 2006). In one such study, tagged fruits of three invasive tree species noted for wind-dispersal (*Ailianthus altissima*, *Acer negundo* and *Acer platnoides*) were released in the Spree River of Berlin, Germany, and directly observed to determine buoyancy (Saumel and Kowarik 2009). Approximately one quarter of the fruits of each species floated 1.2 km within 3 hours. Despite marked differences in the fruit morphology of each species, there were no interspecific differences in the water dispersal capacity of the differently shaped seeds.

Seeds and viable fragments of non-aquatic plant material can accumulate in aqueous environments through primary dispersal directly into water or by secondary movement spurred by animals, wind, or rain wash, often assisted by gravity (Kaproth and McGraw 2008). Given that all of the species in this study are non-aquatic, the use of water as a dispersal vector would likely be used on an opportunistic basis, rather than as a necessary part of the species' reproductive lifecycle. Opportunism is certainly a 'trait' that would be beneficial to exotic species if they are to become invasive. Given that the invasive species studied here are continentally widespread, they may be more likely to be distributed within or near riparian zones (compared to the narrowly-distributed non-invasive species) and thus are more likely to release their propagules into water bodies. There may also be morphological or physiological adaptations in the species' propagules that enable the invasive species to have increased buoyancy in water and/or survival under periods of water immersion, leading to dispersal across longer distances compared to propagules of non-invasive species. Further study exploring these factors in the context of species invasiveness will help to elucidate the implications of water-dispersal for invasive spread.

Might the link between invasiveness and water dispersal of propagules have been generated because water dispersal has been more readily observed in invasive compared with non-invasive species given the wide distribution of the former? I believe this is unlikely given that my surveys of the literature for dispersal information on the non-invasive species in the present study were comprehensive; furthermore, the non-invasive species are well-known species that have been the focus of much study (e.g. *Passiflora coccinea*, see: Wirth and Leal 2001, Fischer and Leal 2006, Leal *et al*. 2006).

Water dispersal of propagules may be of further importance to invasive plant species within Australia as many parts of the continent receive widespread seasonal flooding events each year following rain inundation. These floodwaters rise and sweep across the landscape, often moving a great distance over a short period of time, before the water is absorbed into the landscape or channelled into rivulets. Once the water has receded, the ground left in the wake of the flood is often highly disturbed, with many layers of soil, run-off nutrient and plant material mixed together. Invasive plants able to capitalise on such events by having propagules pre-adapted to water dispersal would not only be able to spread far across the landscape using flood tides but also establish quickly in the wake of the newly disturbed landscape, as disturbance has been positively linked to invasive species establishment in Australia (e.g. Lake and Leishman 2003, Leishman and Thompson 2005).

Intriguingly, the plant traits leaf size and maximum plant canopy height did not differ significantly between the closely-related invasive and non-invasive species in this study. Although there is some evidence linking increased canopy height to increased invasiveness in exotic species (Pyšek *et al*. 1995, Goodwin *et al*. 1999), other studies that considered canopy height found no evidence of such relationship (Hamilton *et al*. 2005, Lloret *et al*. 2005, Cadotte *et al*. 2006). In a similar way, larger leaves have been previously linked to increased invasiveness among groups of exotic species (e.g. Williamson and Fitter 1996a, Lloret *et al*. 2005), but these studies used vastly different approaches in their species comparison as well as using entirely different suites of plant species established in different regions of the world (e.g. naturalised exotic species distributed across five Mediterranean islands, Lloret *et al*. 2005). In the context of previous findings for Australia, specific leaf area (a plant trait found to shift in coordination with leaf size, see: Ackerly and Reich 1999, Villar and Merino 2001) has been found to differ significantly between exotic and native species, with the specific leaf area of invasive exotic species found to be consistently higher than that of non-invasive exotic species, as well as native species (Lake and Leishman 2004). That study investigated the traits of exotic species present in urban bushland remnants within the

Sydney region; therefore, habitat type and spatial scale may be influencing factors in which this plant trait is found to be important for the exotic species of Australia (Collingham *et al*. 2000, Lloret *et al*. 2004). A future direction for this research, given that there is an established growth trade-off between leaf size and leaf number in vascular plants (Kleiman and Aarssen 2007), could be an investigation exploring the mean number of leaves a mature invasive plant produces, and the height at which leaves are photosynthesizing, in comparison to co-occurring non-invasive exotic plants. A study such as this could yield very interesting results, especially when examined in the context of overall plant growth and photosynthetic functioning (e.g. total C produced, net gain of plant biomass over time).

I found that smaller seed mass was not significantly related to invasiveness in this study. It is interesting to note that the non-significant seed mass finding of this study contrasts with previous findings for Australia (Hamilton *et al*. 2005). One potential explanation for this disparity is that the invasive and non-invasive plant species used in this study were selected for comparison using an entirely different methodology compared to the species used in Hamilton *et al*. (2005), which were primarily chosen based on their co-occurring presence within Royal National Park, New South Wales and then scaled up to the larger scale of continental Australia. Furthermore, the present study considered the mean seed mass of each of the exotic plant species. Perhaps a comparison of intraspecific variation in seed mass between invasive and non-invasive species could be useful in determining whether increased seed mass variation can account for species invasiveness. A study of such variation would need to take into account the possibility of both local adaptation across the introduced range as well as the capacity for phenotypic plasticity.

While seed mass was found not to be a significant predictor of invasiveness in this study, other seed attributes might still play an important role in driving plant species invasiveness. For instance, attributes of seed germination are known to vary considerably among species (e.g. seed dormancy within the seed bank). In addition, how seeds grow and develop into seedlings might also be a factor linked to invasiveness given the substantial variation in such traits expressed by plant species (e.g. seedling height, seedling specific leaf area, stem thickness). In the following chapters of this thesis, I explore attributes of seed germination and seedling growth in relation to species invasiveness.

Chapter 4

Investigating relationships between seed survival in the soil and invasion success in exotic plant species within the introduced range

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4.1 INTRODUCTION

Only a subset of exotic species that establish naturalised populations in new regions spread widely to become invasive (Williamson and Fitter 1996). Nevertheless, this subset of species often causes significant environmental and socio-economic impacts (Pimentel *et al*. 2005, Pyšek and Richardson 2010, Vilà *et al*. 2010, 2011). Understanding how exotic plant species shift from naturalisation to invasion is vital for managing the spread of invasive species (Richardson *et al*. 2000). One approach for understanding this shift is to identify plant functional traits that distinguish invasive species from non-invasives (Kolar and Lodge 2001, Pyšek and Richardson 2007, van Kleunen *et al*. 2010). Previous work on invasive plants in Australia has shown that high specific leaf area and increased investment in seed dispersal structures lead to successful invasion (Hamilton *et al*. 2005, Murray and Phillips 2010). However, we are still a long way from fully understanding the mechanisms underpinning the successful spread of invasive plant species.

When exotic plants are introduced to new regions, their seeds are likely to encounter novel fungal species in the soil compared with the fungal flora of soils of their native ranges (Blaney and Kotanen 2001). Indeed, soil-borne fungi are ubiquitous; within one gram of soil, several hundred metres of fungal hyphae can be found (Leake *et al*. 2004). Interactions between germinating seeds and soil-borne fungi can have a range of effects in the context of plant invasions. A beneficial effect occurs when the growth of seedlings and adults of exotic plant species is promoted in the introduced range (compared with the native range) via successful, novel symbiotic mycorrhizal interactions (Marler *et al*. 1997, Reinhart and Callaway 2006). The process might involve release from attack by particular soil pathogens in the native range (i.e. the enemy release hypothesis, Mitchell and Power 2003, Torchin and Mitchell 2004). In contrast, however, exotic plant seeds are open to attack from pathogenic fungi (Blaney and Kotanen 2002). It is widely documented that seeds in general often suffer high mortality rates in soil, largely from pathogenic surface-contaminating fungi (Kirkpatrick and Bazzaz 1979, Leck *et al*. 1989, Keane and Crawley 2002). Pathogenic fungi are species which actively attach to a host plant and consume nutrients from the plant, either by breaking down living plant tissue using toxins and depolymerising enzymes (Oliver and Ipcho 2004), or by spreading throughout the living tissue and passively diverting nutrients away from the host plant (Glazebrook 2005). Such destructive encounters have important implications for distinguishing between invasive species and non-invasives in the naturalisation to invasion transition. For some exotic plant species, for instance, pathogenic fungi may act as an inhibitory barrier and prevent populations establishing and increasing to over-abundance at new sites in the introduced range because of seed mortality in the soil. In contrast, exotic plant species that produce persistent seed banks by better surviving the attacks of soil-borne fungi will have an advantage in transitioning beyond a naturalised state to become invasive.

In the present study, seed survival between invasive and non-invasive exotic plant species was compared in a common garden experiment (i.e. where individuals from different localities are raised under the same natural conditions in a field setting (Garland and Adolph 1991)). A seed burial experiment employing seven pairs of congeneric contrasts between invasive and non-invasive species was performed under field conditions. The purpose of the study was to determine whether a higher rate of seed survival is found in the invasive species in each pair compared with the non-invasive species across the congeneric contrasts. The contrasts were selected such that the species in each pair (i) originated from the same donor continent, (ii) shared similar growth form and habitat occurrence and (iii) had similar residence times in Australia. The addition of fungicide was included as an experimental treatment to test the predictions that seed survival is higher in the presence of fungicide and that a larger increase in seed survival in the presence of fungicide should be observed in non-invasive species if soil-borne fungi play a significant role in reducing their potential for invasiveness in the introduced range. In addition, given that interspecific variation in seed mass has been linked to variation in seed bank longevity among species (Thompson *et al*. 1993, Funes *et al*. 1999), the seed mass of each of the study species was measured and seed mass measurements were included as covariates in the analytical procedures. In this way, differences in seed mass can be accounted for among species as a potential variable underpinning seed survival.

4.2 METHODS

4.2.1 INVASIVE VS. NON-INVASIVE CONGENERIC CONTRASTS

Seed survival was compared between an invasive and a non-invasive exotic plant species in each of seven congeneric pairs of species (Table 4.1). Each congeneric pair was selected to comprise a naturalised invader that has spread rapidly and widely in Australia contrasted with a non-invasive congener that has not been recorded as noxious or a weed of agriculture or the environment and, in spite of widespread ornamental or agricultural planting, has never been recorded as spreading invasively in Australia (Randall 2007). Using the species selection criteria outlined in Chapter 3, I ensured that the invasive and non-invasive species in each pair differed substantially in the extent of invasiveness across Australia, with geographic range sizes of non-invasive species measuring at least ten times smaller than the ranges of invasive congeners. Range size data (as area of occupancy, see Hamilton *et al*. 2005) were obtained from herbarium records maintained at Australia's Virtual Herbarium.

Since long residence time is an important predictor of invasiveness in exotic plant species in Australia (Hamilton *et al*. 2005, Harris *et al*. 2007, Phillips *et al*. 2010a), both the invasive and non-invasive species in each contrast were selected with similar residence times. Residence times in all species and contrasts were a minimum of 60 years (e.g. Murray and Phillips 2010), a period that with current knowledge adequately covers short lag times from introduction to first evidence of invasive spread for plant species (Hobbs and Humphries 1995, Daehler 2009). Residence time for each species was calculated as the year of analysis (2011) minus the earliest year of introduction (Hamilton *et al.* 2005). The Department of Agriculture, Fisheries and Forestry Census of Cultivated Plants 2009 provided data on the earliest year of introduction for each species.

Table 4.1. Invasive and non-invasive exotic plant species in each of the seven congeneric contrasts. Time is minimum residence time (years).

Genus	Species	Family	Status	Origin	Growth form	Time
Aristolochia	*elegans*	Aristolochiaceae	Invasive	South America	Vine	113
Aristolochia	*grandiflora*	Aristolochiaceae	Non-invasive	South America	Vine	125
Coreopsis	*lanceolata*	Asteraceae	Invasive	North America	Herb	150
Coreopsis	*grandiflora*	Asteraceae	Non-invasive	North America	Herb	60
Lonicera	*japonica*	Caprifoliaceae	Invasive	Asia	Shrub	193
Lonicera	*fragrantissima*	Caprifoliaceae	Non-invasive	Asia	Shrub	108
Paspalum	*dilatatum*	Poaceae	Invasive	South America	Grass	134
Paspalum	*fasciculatum*	Poaceae	Non-invasive	South America	Grass	78
Passiflora	*foetida*	Passifloraceae	Invasive	South America	Vine	167
Passiflora	*coccinea*	Passifloraceae	Non-invasive	South America	Vine	167
Salvia	*coccinea*	Lamiaceae	Invasive	South America	Herb	159
Salvia	*splendens*	Lamiaceae	Non-invasive	South America	Herb	167
Solanum	*betaceum*	Solanaceae	Invasive	South America	Shrub	126
Solanum	*torvum*	Solanaceae	Non-invasive	South America	Shrub	80

Invasive and non-invasive species in each pair were selected such that they originated from the same donor continent and were of the same growth form (data from Phillips *et al*. 2010a). Within each pair, both species overlapped in range and co-occurred in habitat within Australia, rather than contrasting species from vastly different areas and habitats and thus potentially exposed to a different suite of environmental conditions. Co-occurrence information was sourced from a range of botanical records including the Flora of New South Wales online database PlantNet. Congeneric species pairs were matched by habitat using the IBRA bioregion classification (v. 16.1), a system that provides information on differentiated regions within Australia that are defined using common environmental characteristics including geology, topology, climate and plant and animal communities (Thackway and Cresswell 1995).

4.2.2 SEED SURVIVAL MEASUREMENTS

The seed burial experiment was performed in a common garden experiment in open-canopy dry sclerophyll woodland at the Faulconbridge Ecological Research Station, in the Blue Mountains region of New South Wales (latitude 33°42'05" S, longitude 150°31'34" E, elevation 470 m), Australia. The area has low nutrient, clayey to sandy soil and receives an average of 200 - 300 mm of rainfall during Spring season and is typical of large tracts of native woodland throughout eastern Australia. All of the study species are known to grow in this woodland habitat and there are a multitude of pathways by which seeds from naturalised populations can disperse to these woodland locations. This experiment explicitly addressed the question; if seeds of invasive and non-invasive congeners reach the soil of woodland habitat at the same time, does the invasive species demonstrate higher seed survival than the non-invasive species?

Fresh seed of each of the study species was sourced from commercial seed suppliers from three naturalised populations within Australia. For each species, 30 seeds were weighed (to µg precision on a LIBROR-AEL-160 electronic analytical balance, Shimadzu, Japan). Seed mass was measured prior to the experiment as the seed coat plus embryo and endosperm, with all dispersal structures removed prior to weighing. Seed bags used to contain the seeds in the soil during the experiment were constructed from a single nylon tough cloth with the outer seams sealed completely using stainless steel staples. A 4 m x 4 m grid was created at the study site with 10 cm deep holes dug at

50 cm intervals along the grid. At each interval, one randomly selected seed bag was buried below the soil surface. Each bag was labeled and filled with 20 randomly selected seeds of a single species and a mix of 450 ml sieved field soil from the experimental study region and 50 ml of fine grade sterile vermiculite. Thus, each bag contained only the seeds of one species. The small quantity of vermiculite was added to each bag to promote water diffusion through the cloth membrane to avoid seed desiccation. Twenty was selected as an appropriate number of seeds for each seed bag to reflect realistic seed bank densities that might occur for the study species and also to prevent seed-to-seed contamination by pathogenic fungi, an effect that has been found to occur more readily with higher density seed treatments (van Mourik *et al*. 2005).

All seeds used in the experiment were surface sterilized by inundation in a 10% solution of sodium hypochlorite (NaOCl) for ten minutes in order to remove any potential pre-existing pathogenic contamination that could bias the survival rates of seeds in the experiment. The seed bags were then placed into one of two treatments: (i) a control, where the seed bag was saturated in water before burial, and (ii) a fungicide treatment, where the seed bag was saturated in fungicide solution before burial. The fungicide treatment was a 1:100 solution of Captan fungicide (*N*-trichloromethylthio-4-cyclohexene-1, 2-dicarboximide) from 48.9% pure wettable powder. Captan is a non-systemic heterocyclic nitrogen fungicide used against a diverse range of fungi including *Botryis, Fusarium, Fusicoccum*, and *Pythium* (Sharvelle 1961, Torgeson 1969, Martinez *et al*. 1998, Blaney and Kotanen 2001) and has been noted for its efficacy against seed-rotting fungi (Neergaard 1979). The seed bags were buried in the field at the beginning of Spring season (September 2009) early in the natural cycle of seed dispersal. After 12 weeks in the soil, all seed bags were excavated from the site and transported intact to the greenhouses at the University of Technology Sydney. The excavated seed bags were opened and for each bag, the inner soil contents were spread evenly over sterilized potting mix in a pot (95 mm x 95 mm x 90 mm). Pots were exposed to optimum temperature, light and water conditions and rotated across greenhouse benches every three days for an additional 3 months. Surface soil agitation was applied every 2 weeks to mimic natural disturbance and encourage deeper-buried seeds to germinate. A census of the total number of germinated seeds (i.e. seeds in which the radicle had penetrated through seed coat) for each bag was performed at the end of the 3-month period. In a number of excavated bags, seeds had already germinated before greenhouse treatment (i.e. the radicle had penetrated through the seed coat); these germinated seeds were removed and added to the total number of seeds that germinated in the greenhouse in the following months. All remaining seeds in each bag that had not germinated were decomposed to such a state as to be clearly dead with no further possibility of germination. Thus, seed survival was measured for each of the species as the number of seeds germinated from the 20 seeds in each replicate for each of the two experimental treatments.

4.2.3 STATISTICAL ANALYSIS

The observed variation in seed survival was modelled in relation to explanatory variables using generalized linear mixed models with the function glmer (library lme4) in R package version 2.14.2011-10-24 (R Development Core Team 2011). Variation in seed survival (the response variable) was modelled as a function of invasive status (a fixed factor, invasive or non-invasive), genus (a random factor, membership in one of seven genera), fungicide treatment (a fixed factor, fungicide added or control with no fungicide) and the continuous covariate seed mass (ln-transformed prior to analysis). Seed mass was included as a covariate given that larger seed mass has been found to significantly improve the survival rate of buried seeds (Moles *et al*. 2003). I specified a binomial error structure with a logit link in models as seed survival was measured in the form of proportion data.

The aim of the analysis was to build a minimum adequate model to explain potential variation in seed survival (Crawley 2007). The full model was fitted first, which included the covariate seed mass and the main effects of invasive status, genus and fungicide treatment and all two-way and the three-way interactions. Following this was the process of model simplification, by inspecting the parameter estimates (using Wald Z tests) and removing the least significant terms starting with the highest-order interactions. After the removal of a term from the model, the initial model was compared with the reduced model using Akaike's Information Criterion (AIC). If the reduced model had a lower AIC value than the initial model, the term was omitted from the next round of analysis and the process of model simplification continued. To compare models with different structures, the Restricted Maximum Likelihood Method was exchanged for the Maximum Likelihood Method for comparing AIC values (Bolker *et al*. 2009). Log-likelihood ratio tests were used to test the significance of the change in deviance resulting from the removal of random factors and the covariate during model simplification. Once the minimum adequate model was identified, I then tested the model for overdispersion, which occurs when there is more variability around a model's fitted values than is consistent with a binomial formulation. To do this, an observation-level random effect was fitted to the model. This factor had 0 variance in the model and hence the model was not overdispersed.

4.3 RESULTS

The model simplification procedure produced a minimum adequate model that retained several explanatory variables linked to seed survival. There was a highly significant main effect of invasion status on seed survival such that seed survival was higher in the invasive species (parameter estimate = 1.97, S.D. = 0.42, Z = 4.69, *P* <0.001; Fig. 4.1a). There was also a significant main effect of fungicide treatment on seed survival with seed survival higher in seeds treated with fungicide (parameter estimate = 0.54, S.D. = 0.21, Z = 2.53, *P* <0.05; Fig. 4.1b). These main effects were superseded by a significant interaction between fixed factors such that the fungicide treatment improved seed survival in general but there was a noticeably stronger effect observed in non-invasive species (parameter estimate = 0.71, S.D. = 0.30, Z = 2.39, *P* <0.05; Fig. 4.1c). Removal of two random factors during model simplification produced significant changes in deviance, thus genus (χ^2 = 5.60, d.f. = 1, *P* = 0.02; variance = 1.32, standard deviation = 1.55) and the genus x invasion status interaction (χ^2 = 22.17, d.f. = 1, *P* <0.0001; variance = 0.44, standard deviation = 0.66) were retained in the final model. The genus x invasion status interaction arose because seed survival was significantly higher in invasive compared with non-invasive species within six of the seven congeneric pairs including *Aristolochia*, *Coreopsis*, *Lonicera*, *Paspalum*, *Passiflora* and *Salvia*, but not in the remaining contrast *Solanum* (Fig. 4.2). A key finding from model simplification was that removal of the covariate seed mass resulted in a non-significant change in deviance and thus it was not retained in the minimum adequate model (χ2 = 0.51, d.f. = 1, *P* = 0.48). In fact, seed mass differences between invasive and non-invasive species varied among the pairs, such that seeds were heavier in some contrasts and lighter in others (Fig. 4.3).

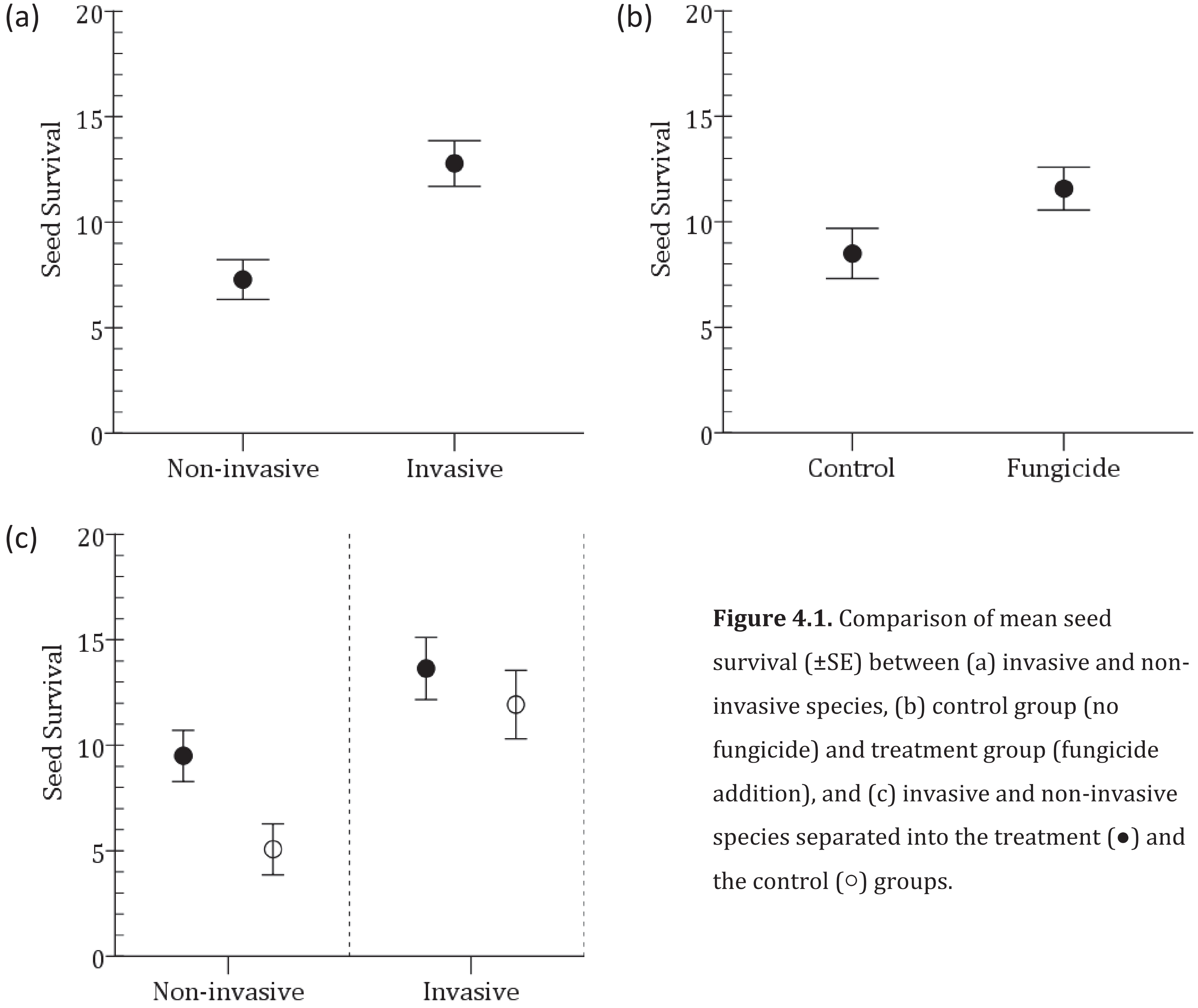

Figure 4.1. Comparison of mean seed survival (±SE) between (a) invasive and non-invasive species, (b) control group (no fungicide) and treatment group (fungicide addition), and (c) invasive and non-invasive species separated into the treatment (●) and the control (○) groups.

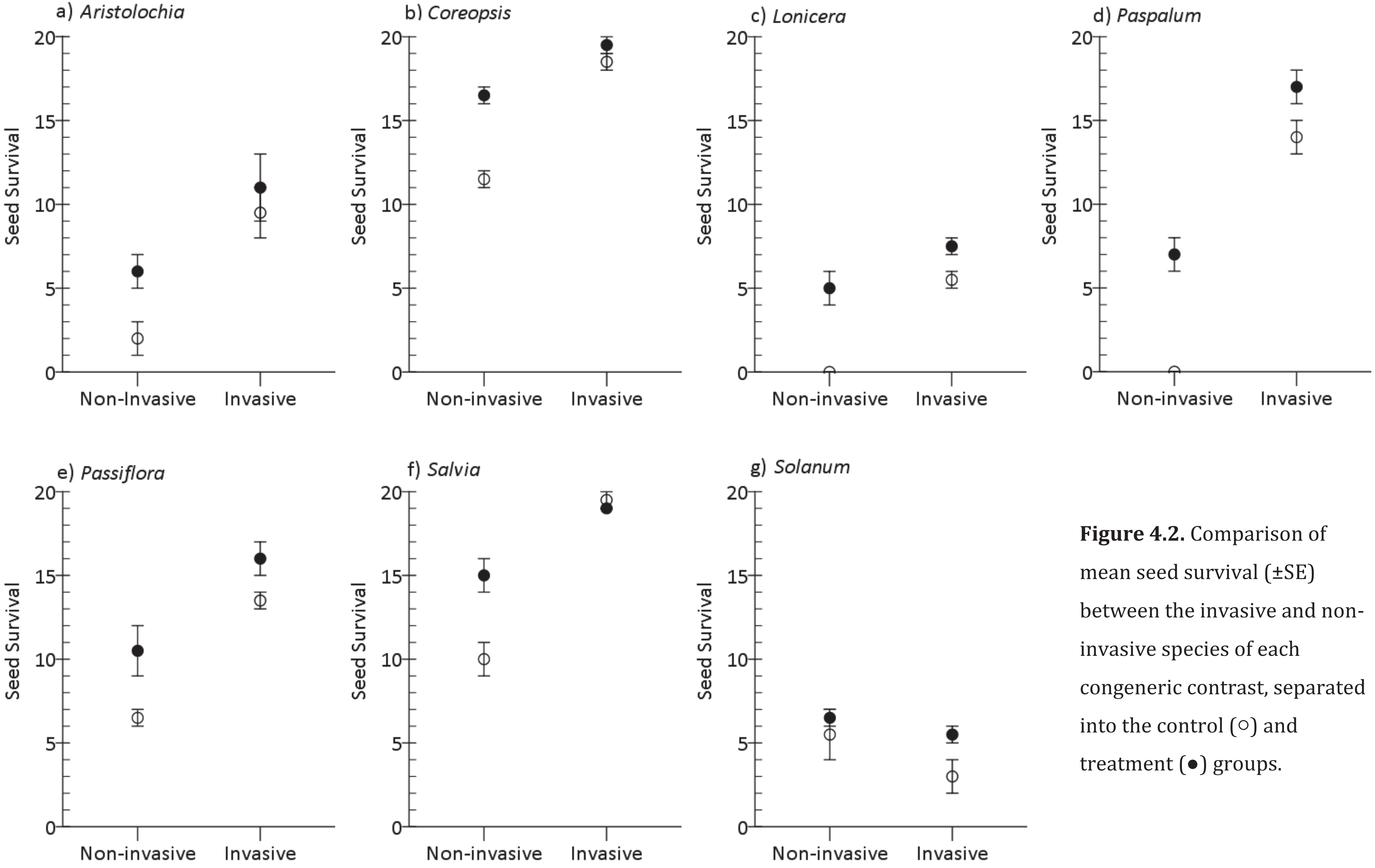

Figure 4.2. Comparison of mean seed survival (±SE) between the invasive and non-invasive species of each congeneric contrast, separated into the control (○) and treatment (●) groups.

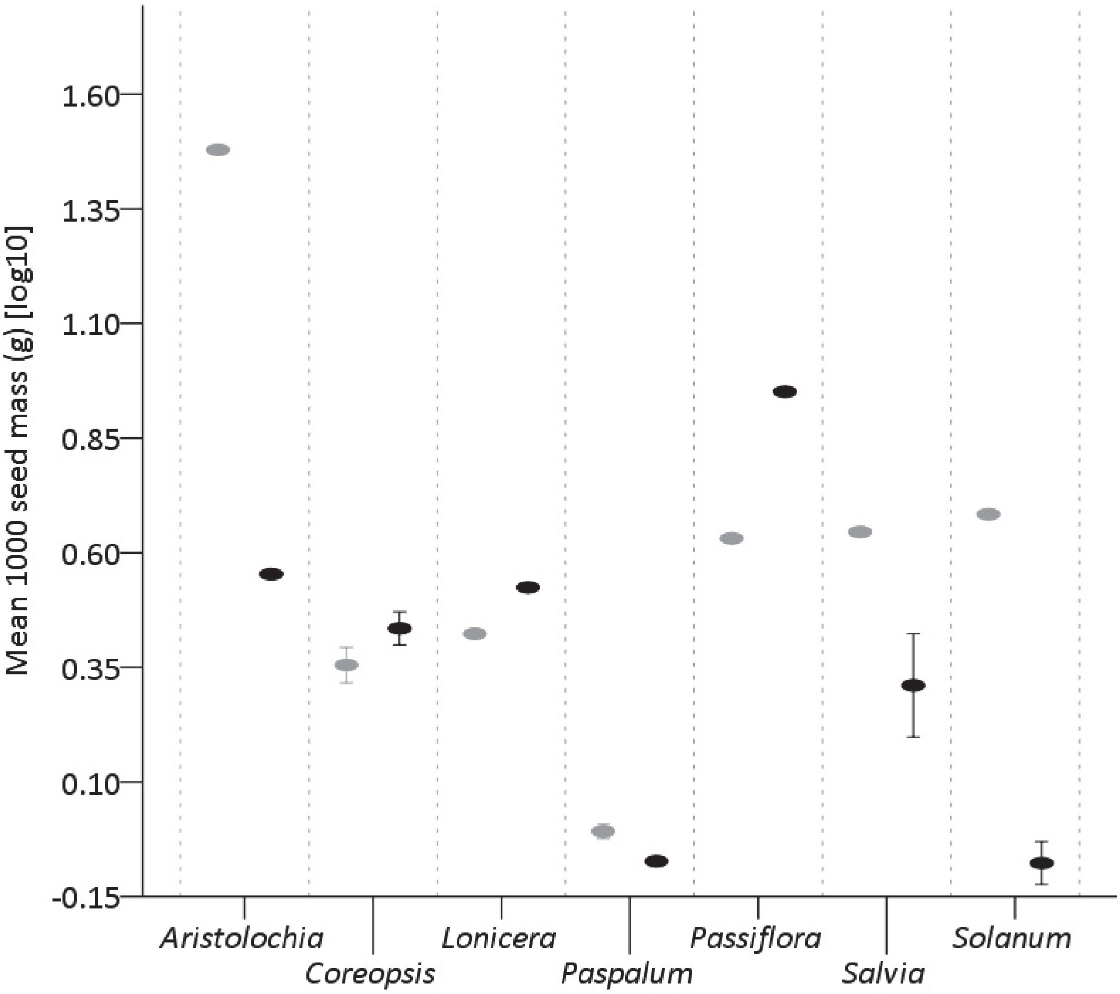

Figure 4.3. Comparison of mean seed mass (±SE) between the invasive (dark bars) and non-invasive (light bars) species of each congeneric contrast. Species with low variation in seed mass do not show error bars.

4.4 DISCUSSION

An important link was found between invasiveness in exotic plant species and a higher rate of seed survival in the soil. The findings of this study support the notion that seed survival in the soil may play a key role in facilitating the transition from naturalisation to invasion. Importantly, the statistical modelling showed that higher seed survival in invasive species was not promoted by interspecific variation in seed mass. Indeed, in congeneric pairs where seed survival was higher in the invasive species both larger seed mass (e.g. *Lonicera*) and smaller seed mass (e.g. *Aristolochia*) were found in the invasive species (Fig. 3). A broad mechanistic explanation of higher seed survival in the invasive species therefore cannot be based on large or small seed size facilitating seed survival in the soil.

Seed survival was found to be higher in the presence of fungicide in general and, in particular, a larger increase in seed survival in the presence of fungicide was observed in the non-invasive species. These findings suggest soil-borne fungi may be limiting the survival of seeds of exotic plant species in an introduced range but, critically, the larger effect observed on non-invasive species indicates that fungal pathogens in the soil may play a role in reducing the potential of non-invasive species for invasive spread. One consideration for this pattern is that the Captan fungicide may also be having a repelling effect on soil biota other than fungi. Further investigation in to the effect of Captan fungicide on the broader soil community is certainly merited.

The genus *Solanum* provided an exception to this pattern for higher seed survival rates in invasive species. Previous work investigating survival of seeds of members of the *Solanaceae* family against pathogenic attack revealed that many genera and species of the family have anti-microbial, low-molecular-weight secondary metabolites (sesquiterpenoid phytoalexins) present in their tissues. These metabolites act as a protective agent against pathogenic interference, including against pathogenic soil fungi (Kuc 1995). The production of this anti-microbial metabolite by both non-invasive *Solanum torvum* and invasive *Solanum betaceum* might have been expected to result in similar levels of seed survival. However, these two species had the lowest seed survival rates across the congeneric pairs which suggest that these species might not have been afforded the protection of anti-microbial metabolites. Indeed, studies have shown that initial production of phytoalexins by not-yet germinated seed tissues is dependent on the occurrence of prolonged high soil moisture levels (Halloin 1983). The dry climate and the sandy soils of the study site, which do not hold moisture well, may have led to an absence of this important protective metabolite. This would have caused the seeds of both Solanaceaous species to be more susceptible to pathogenic attack.

Another contributing factor to the higher seed survival rate in invasive species relates to properties of the seed coat (e.g. thickness, permeability). The physical and chemical composition of a seed ultimately govern both its susceptibility to predation by invertebrates including ants, millipedes, isopods, earthworms and other fauna (Baskin and Baskin 1998, Eisenhauer *et al*. 2009) and decomposition due to environmental intolerance of frost or damp conditions. Seeds with better physical and chemical adaptations to protect against these antagonistic processes will be able to survive longer in the soil (Hallion 1983). These factors remain to be tested for the study genera, and their future examination will add important information to the central findings of the research presented in this study.

4.5 CONCLUSION

Studies such as this, with a focus on plant functional traits for which new field data need to be collected over time using manipulative experimentation, reflect a trade-off between effort involved in the collection of fresh field data and the number of species that can be realistically examined in such studies (e.g. Perglová *et al*. 2009, Grotkopp *et al*. 2010). These sorts of studies, which involve rigorous protocols for species selection in an evolutionary context (i.e. congeneric contrasts), combined with informative studies using extremely large (i.e. hundreds to thousands of species) databases involving traits for which data are readily available in the literature (Castro *et al*. 2005, Herron *et al*. 2007, Küster *et al*. 2008, Hejda *et al*. 2009, Pyšek *et al*. 2009, Murray and Phillips 2010), are crucial in our efforts to identify plant functional traits that explain invasiveness in exotic plant species. Both approaches have the potential to improve our fundamental understanding of biological invasions (Pyšek and Richardson 2007). In the field setting used in this study, I was able to demonstrate that under similar environmental conditions the seeds of some invasive species are better equipped to survive in soil than non-invasive species, providing experimental evidence for a naturalisation-to-invasion advantage in invasive exotic plant species.

Chapter 5

Relationships between seed germination and plant species invasiveness

5.1 INTRODUCTION

Seeds represent an important resource investment for plant species, as their survival (see Chapter 4) and germination are intimately linked to population persistence within a region (Cohen 1966, Brown and Venable 1986, Donohue *et al*. 2010). Exotic plant species that employ seed germination strategies which increase the likelihood of successful seedling establishment in new regions will be well positioned to form persistent populations, thus possessing a greater chance of expanding their distribution in the introduced range and of making the transition from naturalization to invasion.

Baker (1974) compiled the first list of plant life-history traits which he believed encapsulated the 'ideal' invasive species. His comprehensive list included, among other traits, rapid and profuse seed germination. Indeed, of the wide spectrum of plant life-history traits found to be associated with increased species invasiveness, there is an emerging notion that both rapid and profuse germination could be fundamental species traits linked to the establishment and geographic spread of exotic plant species (Klink 1996, Pérez-Fernández *et al*. 2000, Goergen and Daehler 2001, Gruberová *et al*. 2001, Mihulka *et al*. 2003, van Kleunen and Johnson 2007, Fisher *et al*. 2009, Flory and Clay 2009, Schlaepfer, *et al*. 2010). Species that germinate rapidly are likely to produce larger seedlings compared to species which do not germinate as rapidly (van Kleunen and Johnson 2007). Profuse germination increases the abundance of a species within a region, therefore increasing the likelihood of species survival and invasiveness (Lockwood *et al*. 2005). An exotic species that exhibits accelerated population growth via rapid and profuse germination is likely to have a strong competitive and invasive advantage over co-occurring species by suppressing the germination and growth of slower and less-profusely germinating species (Weiner and Thomas 1986, Milberg and Lamont 1995, Verdu and Traveset 2005, Damgaard and Weiner 2008, Chrobrock *et al*. 2011).

Rapid germination is a notably common adaptation found in plants from drought-prone environments, not unlike much of Australia's landscape, which can experience long periods without rain from the coast to the interior of the continent.

Under such circumstances, seeds of invading species must be able to germinate quickly in response to a sporadic rainfall event before the surface soil moisture evaporates (El-Keblawy *et al*. 2009). Invasive plant species that produce seeds which germinate rapidly in response to a sporadic rainfall event will have greater opportunity to colonize open micro-sites, achieving a direct establishment advantage over slower-germinating species (e.g. the 'gap-grabber' concept of Newsome and Noble 1986). Rapid germination can also reduce seed predation and mortality risk in the seed bank by allowing seeds to germinate after a short latency period (Brown and Venable 1991, Donohue *et al*. 2010).

A trade-off with rapid and profuse seed germination is that the favourable environmental conditions which triggered the onset of germination may be transient and may not last for a long enough period of time to support the establishment of healthy seedlings. If a plant produces a cohort of seeds that all germinate simultaneously after rainfall, and an unfavourable environmental event (e.g. a strong heatwave) occurs shortly thereafter, the entire cohort of fragile, newly-germinated seedling progeny is likely to perish (Daws *et al*. 2007). Risk-spreading through staggered germination during the one particular imbibition event as well as increased seed dormancy following the imbibition event can be ideal 'bet-hedging' strategies for exotic plant populations growing in new ranges (Cohen 1966, Venable and Lawlor 1980, Brown and Venable 1986, Venable and Brown 1988, Philippi 1993, Venable 2007). Under this scenario, a bet-hedging plant produces seeds which delay their germination in two ways: the first by extending the length of the germination period (i.e. not producing seeds that simultaneously germinate in a short burst) and the second by having a fraction of seeds remain in a state of dormancy after the environment queue has occurred (Evans *et al*. 2007, Venable 2007, Childs *et al*. 2010). Bet-hedging strategies act as buffers against the quick onset of unfavourable environmental conditions, reducing the risk of seedling death from a 'false start'; that is, seedling mortality during harsh environmental conditions that follow a favourable germination-triggering environmental event.

There have been many single-species studies conducted investigating links between species invasiveness and germination traits (e.g. Lonsdale *et al*. 1988, Bungard *et al*. 1997, Brändel 2004, Krinke *et al*. 2005, Nogales *et al*. 2005, El-Keblawy and Al-Rawai 2006, Kettenring and Whigham 2009), however, comparatively fewer studies have compared native and exotic species for germination differences (e.g. Pérez-

Fernández *et al*. 2000, van Clef and Styles 2001, Chrobock *et al*. 2011). Fewer still have compared germination traits between invasive and non-invasive congeners (e.g. *Atriplex* spp. Mandák 2003, *Oenethera* spp. Mihulka *et al*. 2003, *Ruellia* spp. Cervera and Parra-Tabla 2009). One previous study has used multiple congeneric pairings to compare seed germination traits between invasive and non-invasive exotic species across different plant genera (Schlaepfer *et al*. 2010), but that study was conducted on species populations within the native range and focused on pre-adaptation, therefore potentially not reflecting the germination responses of naturalised populations within the introduced range. In addition, short residence times of some of the 'non-invasive' species used in that study could indicate that the non-invasive species have not yet reached their invasion potential within the target-area of North America and may not truly represent non-invasive species. The earliest herbarium records of 'non-invasive' *Campanula patula* was 1990, *Geranium pratense* was 1992 and *Trifolium medium* was 1995.

In the present study, I use multiple congeneric pairs of invasive and non-invasive species and an integrated approach involving four key seed germination traits to explore the contribution of these traits to exotic species invasiveness. Importantly, I retain the introduction-history, life-history and phylogenetic considerations previously described in this thesis (Chapter 3).

The aim of this chapter was to test four key predictions linking interspecific variation in seed germination to species invasiveness:

(i) The seeds of invasive species will have a shorter time to first germination compared with the seeds of non-invasive species;
(ii) The seeds of invasive species will have a longer overall germination period within the single imbibition event compared with seeds of non-invasive species;
(iii) A higher proportion (but not all) of the seeds of invasive species will germinate compared with the seeds of non-invasive species; and
(iv) A higher proportion of the ungerminated seeds of invasive species will be dormant (and still viable) compared with the seeds of non-invasive species.

5.2 METHODS

5.2.1 SPECIES SELECTION

Congeneric pairs were selected using the species selection framework outlined in Chapter 3 and based on the availability of fresh seed for the experiment. A single pair of an invasive and a non-invasive species was selected from each of the genera *Aristolochia*, *Coreopsis*, *Genista*, *Lonicera*, *Passiflora*, *Salvia* and *Solanum* (Table 5.1).

Fresh seed of each of the study species was sourced from field populations or commercial seed suppliers from three naturalised populations within Australia. For each species, four lots of 50 seeds were weighed (to µg precision on a LIBROR-AEL-160 electronic analytical balance, Shimadzu, Japan) and mean individual seed mass was calculated. Seed mass was measured prior to the experiment as the seed coat plus embryo and endosperm, with all dispersal structures removed prior to weighing.

5.2.2 SEED VIABILITY ASSESSMENT AT THE BEGINNING OF THE EXPERIMENT

Prior to the commencement of the study, seed viability was determined by visual inspection and an unimbimbed squeeze test. A squeeze test is a non-destructive method of determining initial seed viability. To conduct this test, forceps were lightly pressed on either side of the seed and light pressure was imposed on the seed. Seeds were considered viable if the seed coat did not crack, deform or collapse under light pressure (Sawma and Mohler 2002). Following the initial viability assessment, 120 viable seeds for each species were selected for the germination experiment. All viable seeds were surface sterilized by inundating seeds in a 10% solution of sodium hypochlorite (NaOCl) for fifteen minutes in order to remove any potential pre-existing pathogenic contamination that could affect seed germination.

5.2.3 DORMANCY-BREAKING PROCEDURES

Several species in this study have consistent records of prolonged dormancy periods, with seed dormancy periods of some species extending for several months or more (e.g. *Lonicera japonica* and *L. fragrantissima*; Hidayati *et al*. 2000, Shelton and Cain 2002). Many seeds require specific environmental queues that occur under natural conditions (e.g. seasonal temperature shifts, seed coat softening during animal digestion) to break dormancy. As this was an environmentally-controlled experiment performed under

Table 5.1. Invasive and non-invasive exotic plant species in each of the seven congeneric contrasts used in this study.

Genus	Species	Family	Status	Growth form	Mean seed mass (mg)
Aristolochia	*elegans*	Aristolochiaceae	Invasive	Vine	2.055
Aristolochia	*grandiflora*	Aristolochiaceae	Non-invasive	Vine	30.122
Coreopsis	*lanceolata*	Asteraceae	Invasive	Herb	2.693
Coreopsis	*grandiflora*	Asteraceae	Non-invasive	Herb	2.279
Genista	*monspessulana*	Leguminosae	Invasive	Shrub	7.654
Genista	*tinctoria*	Leguminosae	Non-invasive	Shrub	5.383
Lonicera	*japonica*	Caprifoliaceae	Invasive	Shrub	3.344
Lonicera	*fragrantissima*	Caprifoliaceae	Non-invasive	Shrub	2.651
Passiflora	*foetida*	Passifloraceae	Invasive	Vine	8.344
Passiflora	*coccinea*	Passifloraceae	Non-invasive	Vine	7.832
Salvia	*coccinea*	Lamiaceae	Invasive	Herb	2.063
Salvia	*splendens*	Lamiaceae	Non-invasive	Herb	4.421
Solanum	*betaceum*	Solanaceae	Invasive	Shrub	0.839
Solanum	*torvum*	Solanaceae	Non-invasive	Shrub	4.832

glasshouse conditions, the natural environmental queues needed to break dormancy and stimulate germination in *Aristolochia*, *Genista*, *Lonicera*, *Passiflora* and *Solanum* species could not occur in a laboratory setting without intervention. For this reason, I stimulated the seeds of both the invasive and non-invasive within each pair using a variety of genus-specific treatments in order to break physical and physiological seed dormancy. In accordance with previous research, the following treatments were applied to seeds just prior to the beginning of the experiment:

Aristolochia: seeds of both the invasive and non-invasive species were soaked in room-temperature distilled water for a period of 48 hours (Edwards and Leon 2002).
Genista: seed coats of both species were lightly scarified with medium-grade sandpaper (Francis and Rodriguez 1993).
Lonicera: seeds of both species received warm stratification (i.e. warming in moist, sterile vermiculite) followed by cold stratification (Hidayati *et al*. 2000).
Passiflora: seeds of both species were soaked in room-temperature distilled water for a period of 24 hours (Riley 1981).
Solanum: seeds of both species were chilled at 5°C for a period of 24 hours (Hayati *et al*. 2005).

Pilot germination tests revealed that seeds of both invasive and non-invasive species of *Salvia* and *Coreopsis* were able to readily germinate in a laboratory setting following the application of a simple moisture treatment, indicating supplemental dormancy-breaking stimulation was not required for these species.

5.2.4 GERMINATION TRAITS AND THEIR MEASUREMENT

Germination was assessed using twelve replicate petri dishes, each with ten seeds, per species. For each replicate, seeds were placed into a 9 cm Petri dish which was lined with three sheets of sterile filter paper (Whatman Inc, Clifton, NJ). The filter paper was moistened with 5 ml of de-ionised water to simulate an artificial rainfall event. Petri dishes were then carefully sealed with a layer of Parafilm to prevent excess moisture loss and seed desiccation during the experiment. The sealed Petri dishes were placed on shelves of an environmentally-controlled cabinet (Environ Air EA7BH; SRG Cabinet Sales, Greenacre, NSW, Australia). The environmental parameters of the cabinet were set to mimic 24 hour cycles of ambient Spring conditions in south-eastern NSW (based on a standard 30-year climatology) with a day temperature of 22°C and light exposure occurring for 8 hours and then a night temperature of 12°C and darkness occurring for the following 16 hours (Bureau of Meteorology 2011). Petri dishes were randomly rotated between and across shelves every two days to prevent any microclimatic differences within the cabinet biasing the study results. Seed germination was monitored at the same time each day (11am) for the first twenty days of the study period and then monitored every two days for the next 20 days of the study period.

I used visible germination (i.e. radicle emergence from the seed coat) as the indicator of seed germination. Time to first seed germination (hereafter 'first germination') for each species was calculated as the number of days after the experiment commenced until the first occurrence of visible germination within a Petri dish (i.e. if a seed first germinated on the 8th day after the experiment had commenced, the time to first germination for that replicate was 8 days). Length of the seed germination period (hereafter 'germination period') for each species was the number of days from first seed germination to the last day of seed germination. Total seed germination was calculated as the proportion of seeds germinated per 10 seeds in each Petri dish. Seed dormancy was calculated as the proportion of ungerminated but viable seeds per 10 seeds in each Petri dish at the end of the experiment.

5.2.5 SEED VIABILITY ASSESSMENT AT THE END OF THE EXPERIMENT

A Tetrazolium (TTZ) test was applied to all remaining seeds that had not germinated during the study period to assess the viability of ungerminated seeds. This approach was adopted at the end of the experiment as a squeeze test was not appropriate for the imbibed seeds. A TTZ test is a redox reaction whereby viable seed tissues are stained red after prolonged immersion within a clear TTZ solution. If the major organs of the seed (e.g. embryo, endosperm) are observed to be intact and stained red after an immersion period of several hours, the seed is considered to be viable. If no such staining is present, or the seed is found to have visible and significant signs of tissue damage and degradation the seed is considered to be non-viable.

Following the methodology outlined in the *Tetrazolium Testing Handbook* (Peters 2010), a 1.0 g of Tetrazolium red powder was weighed and dissolved in 100 ml of pure distilled water. The pH for the aqueous TTZ solution must be between 6.5 and

7.5 for optimum staining results, therefore a pH meter was used to confirm the pH neutrality of the distilled water. The solution was found to have a pH of 7.0, falling within the acceptable parameters of the test and therefore the addition of a buffering solution was not required. Seeds that were ungerminated at the end of the experiment were carefully bisected across the longitudinal axis and soaked in the 1% TTZ solution. Seeds from different taxonomic families have different temperature and immersion duration requirements in order to show a reaction to the TTZ solution, so each congeneric pair was immersed in solution at different times and temperatures appropriate to the specific requirements of each plant family (Peters 2010).

Following TTZ treatment, individual seeds were examined beneath a light microscope to determine viability. All seeds that were found to be viable (i.e. major organ tissues were intact and stained red) at the end of the experiment (but which had failed to germinate) were categorized as dormant. For each species, seed dormancy was calculated as the proportion of viable, ungerminated seeds per 10 seeds in each Petri dish.

5.2.6 STATISTICAL ANALYSIS

5.2.6.1 DATA NORMALITY

Data for the four germination traits were assessed for normality by performing a series of One-Sample Kolmogorov-Smirnov (K-S) tests. The K-S tests showed that first germination (P = 0.162) and germination period (P = 0.170) were normally distributed, however, exploratory homogeneity tests showed that the variances for both traits were not homogeneous, thereby violating an important assumption of parametric tests. As a result, these two traits were analysed using Generalized Linear Models with a Poisson error structure for count data followed by Tukey's HSD post-hoc test. The K-S tests showed that total seed germination (P = 0.002) and seed dormancy (P = 0.000) were not normally distributed. Following the compelling argument made by Warton and Hui (2011) in regard to transforming proportional data, the data were logit transformed and re-tested for normality (no arcsine square root transformations were used). The data remained non-normally distributed and, as a consequence, the proportional traits were also analysed using Generalized Linear Models with a binomial error structure for proportional data followed by Tukey's HSD post-hoc test. In all cases, invasive status and genus were used as fixed predictor variables and the germination response traits were analysed separately as response variables. As genus was treated as a fixed factor in the analyses to look for interaction effects, analytical outcomes are restricted to the genera in this study and are interpreted as such (Quinn and Keough 2002). All statistical analyses were performed using SPSS Statistics (SPSS Inc, version 20, IBM).

5.2.6.2 THE POTENTIAL INFLUENCE OF SEED MASS ON GERMINATION

Previous work has found that small seed mass can be strongly correlated with accelerated germination (Norden *et al*. 2008). Therefore, the potential for seed mass to influence seed germination was initially investigated within the congeneric pairs. Seed mass data were tested for normality by performing a K-S test and plotting the distribution of the data on a frequency histogram. Although the K-S test returned a non-significant result ($P = 0.148$), upon inspection, the frequency histogram revealed moderate skewness. As a result, seed mass data were log-transformed and the K-S test was reapplied to transformed data as well as replotting the data on a frequency histogram to assess normality. Log-transformed seed mass data were normally distributed and the K-S test significance had decreased further ($P = 0.941$), indicating that transformation improved normality.

A series of exploratory linear regressions were then performed on each of the four germination traits (each treated as a response variable in separate regressions) using log seed mass as the explanatory variable. All four germination traits were not significantly related to seed mass (Table 5.2); therefore seed mass was not used as a covariate in further analyses.

Table 5.2. Linear regressions examining the effect of seed mass on seed germination of exotic species.

Germination trait	Sums of Squares	d.f.	*F*	*P*
First germination	7.760	1	0.537	0.465
Germination period	1.748	1	0.065	0.800
Total seed germination	0.034	1	0.258	0.612
Seed dormancy	1.470	1	1.037	0.310

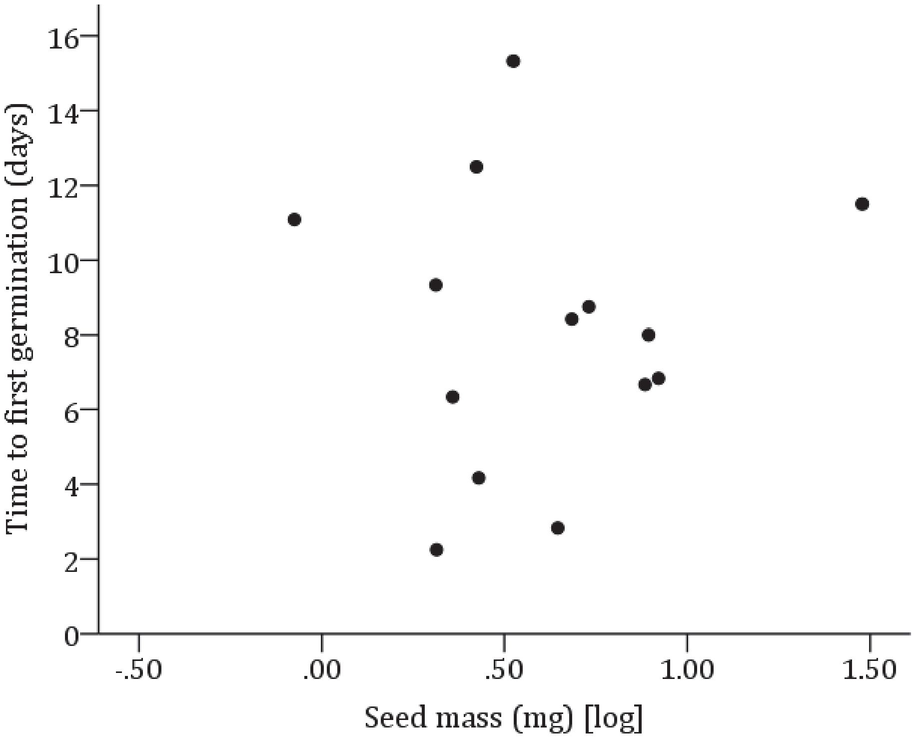

Figure 5.1. First germination as a function of mean seed mass.

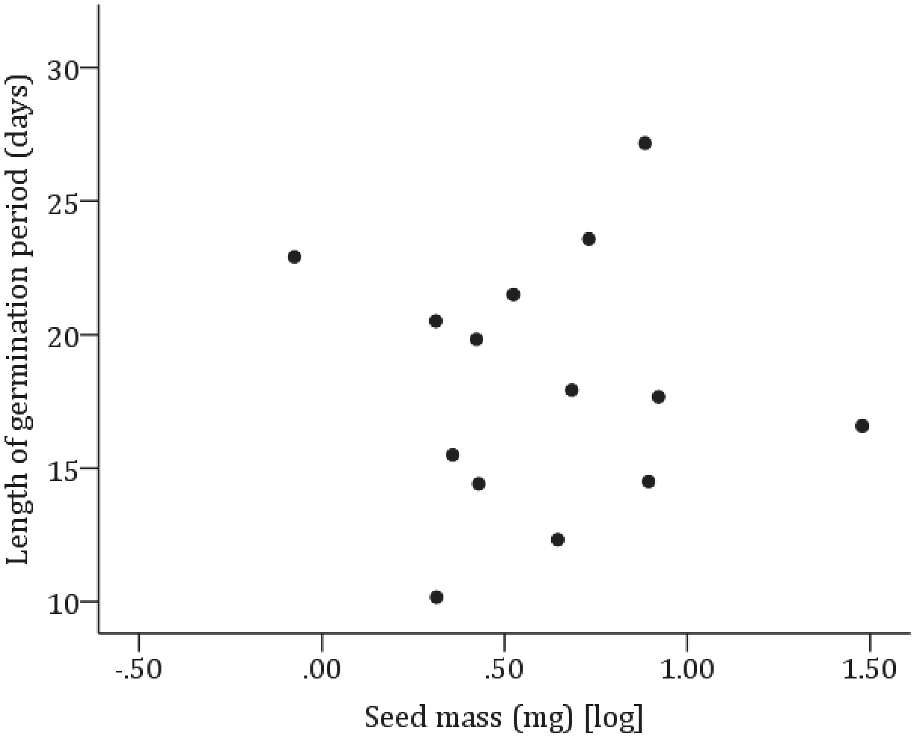

Figure 5.2. Germination period as a function of mean seed mass.

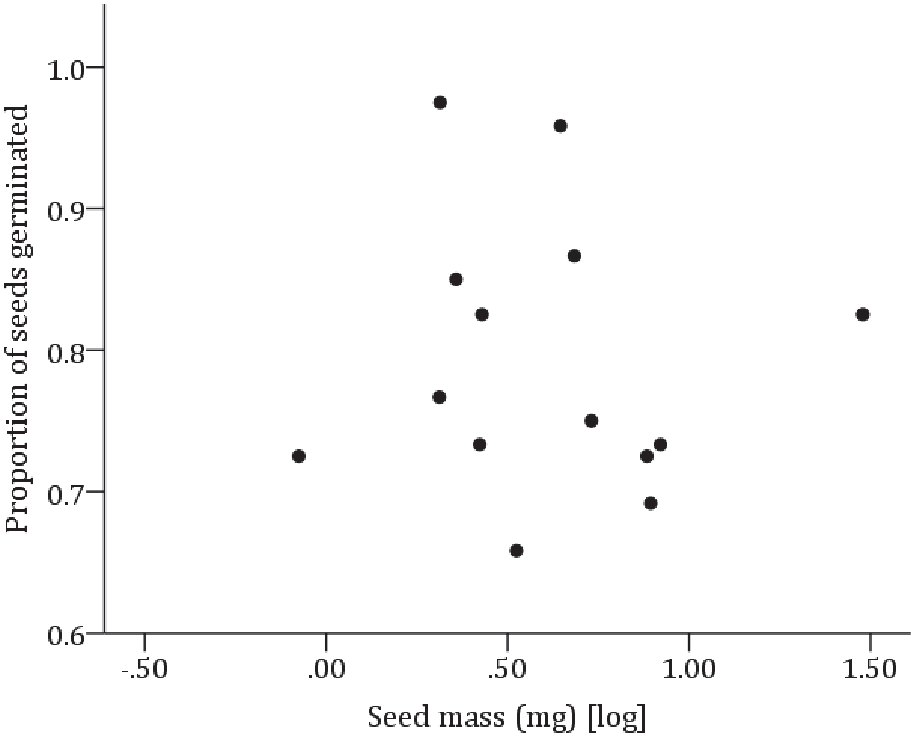

Figure 5.3. Total seed germination as a function of mean seed mass.

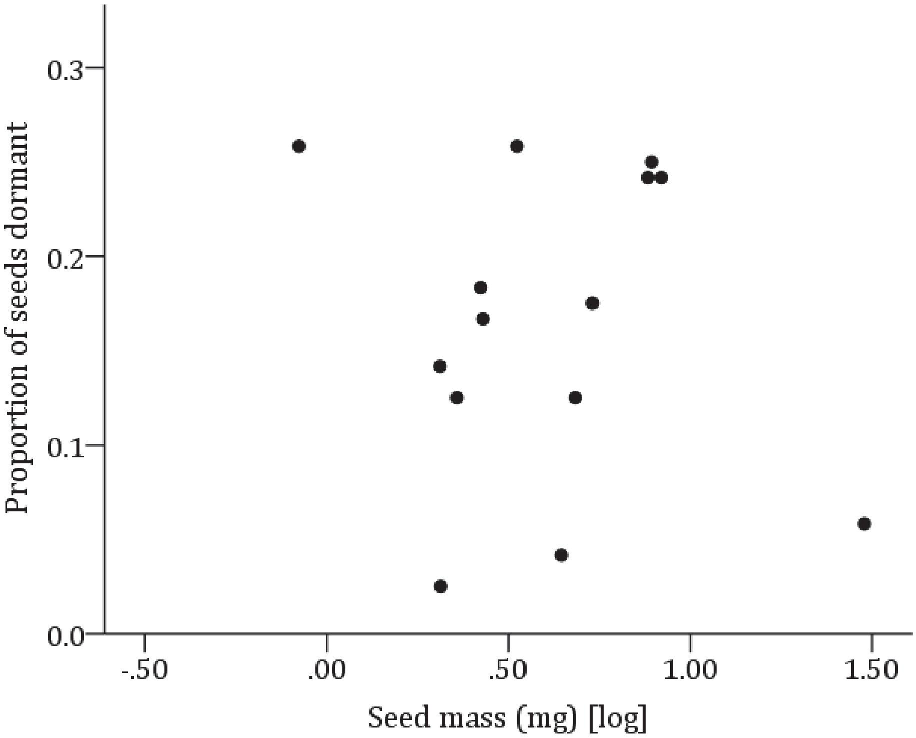

Figure 5.4. Seed dormancy as a function of mean seed mass.

5.3 RESULTS

5.3.1 Time to first germination

The relationship between accelerated germination and plant invasiveness was marginally non-significant (Table 5.3). First germination varied significantly among plant genera (Table 5.3, Fig. 5.5), with seeds of *Salvia* spp. and *Coreopsis* spp. germinating earliest (within the first week) and *Lonicera* spp. germinating latest (up to two weeks later).

Table 5.3. Generalized linear model relating first germination to species invasiveness and taxonomy (genus).

Source	Wald Chi-Square	d.f.	*P*
Status	3.437	1	0.064
Genus	214.083	6	< 0.001
Status x Genus	20.309	6	0.002

A significant interaction occurred between invasive status and plant genus, indicating that first germination varied between invasive and non-invasive species in different ways across the different plant genera (Fig. 5.5). A positive relationship between species invasiveness and accelerated germination was observed within the genera *Aristolochia*, *Coreopsis*, *Genista*, *Passiflora* and *Salvia*. Conversely, a negative relationship between species invasiveness and accelerated germination was observed in the genera *Lonicera* and *Solanum*.

5.3.2 Germination period

There was a significant relationship between increased length of germination period and species invasiveness (Table 5.4, Fig. 5.6). Germination period also varied significantly across the different plant genera (Fig. 5.6). *Salvia* species exhibited a relatively short period of time in which seeds germinated (less than 12 days) whereas the seeds of the genus *Genista* germinated continuously over 26 days.

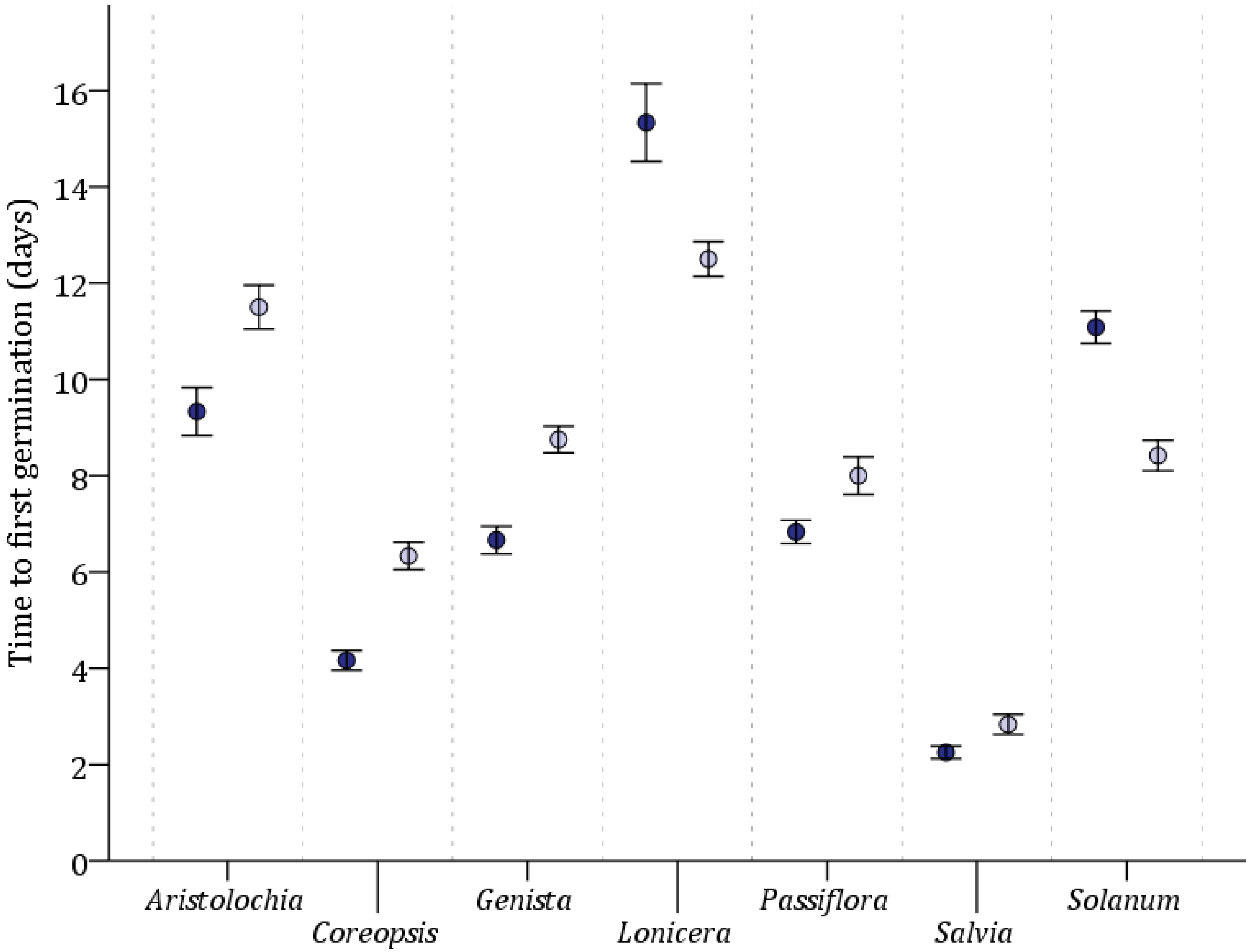

Figure 5.5. First germination (mean ± S.E.) compared across plant genera and as a function of invasiveness. Dark blue circles represent invasive species; light blue circles represent non-invasive species

Table 5.4. Generalized linear model relating germination period to species invasiveness and taxonomy (genus).

Source	Wald Chi-Square	d.f.	*P*
Status	5.461	1	0.019
Genus	161.138	6	< 0.001
Status x Genus	13.501	6	0.036

A significant interaction revealed that germination period differed between invasive and non-invasive species in different ways across the different plant genera (Fig. 5.6). A positive relationship between invasiveness and longer germination period was found in the genera *Aristolochia*, *Genista*, *Passiflora* and *Solanum*. The genera *Coreopsis*, *Lonicera*, *Salvia* showed no relationship between species invasiveness and germination period.

5.3.3 Total seed germination

Total seed germination did not differ significantly between invasive and non-invasive species (Table 5.5). There was, however, significant variation in total seed germination across the different plant genera (Fig. 5.7). *Salvia* species had the highest total seed germination while the genera *Genista*, *Lonicera* and *Passiflora* had the lowest total seed germination. No statistical interaction for total seed germination was observed between invasive status and plant genus.

Table 5.5. Generalized linear model relating total seed germination to species invasiveness and taxonomy (genus).

Source	Wald Chi-Square	d.f.	*P*
Status	1.265	1	0.261
Genus	56.399	6	< 0.001
Status x Genus	7.809	6	0.252

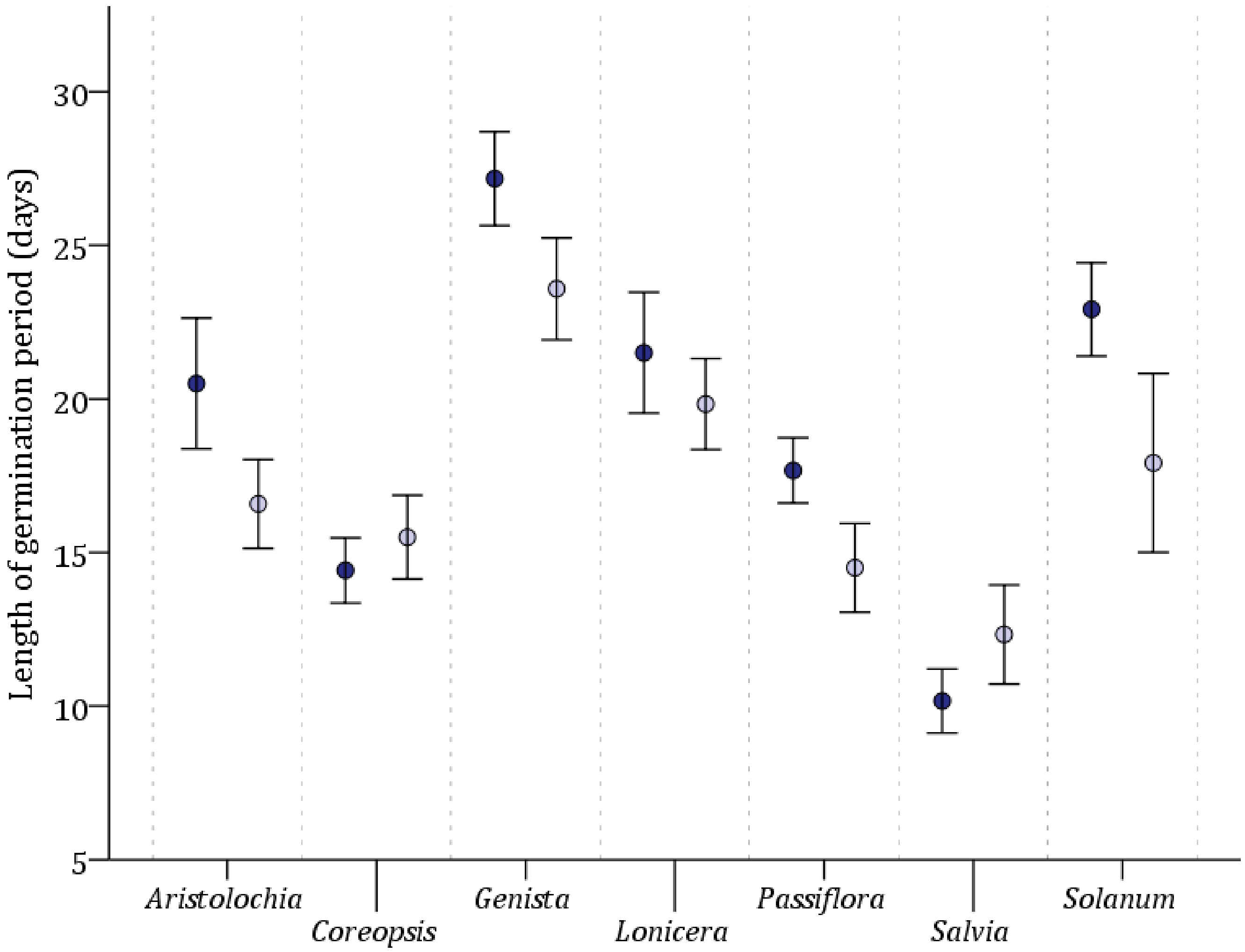

Figure 5.6. Length of germination period (mean ± S.E.) compared across plant genera and as a function of invasiveness. Dark blue circles represent invasive species; light blue circles represent non-invasive species.

5.3.4 Seed dormancy

Invasive species had significantly higher seed dormancy compared to non-invasive species (Table 5.6, Fig. 5.8). There was significant variation in seed dormancy among the different plant genera (Fig. 5.8). The genera *Genista*, *Lonicera, Passiflora* and *Solanum* had the highest seed dormancy while *Salvia* and *Aristolochia* had the lowest seed dormancy. There was no significant interaction between invasive status and genus.

Table 5.6. Generalized linear model relating seed dormancy to species invasiveness and taxonomy (genus).

Source	Wald Chi-Square	d.f.	*P*
Status	4.667	1	0.031
Genus	49.112	6	< 0.001
Status x Genus	7.355	6	0.289

Table 5.7. Summary of germination responses across plant genera. The '↑' symbol indicates response higher value for invasive species compared with non-invasive species, the '↓' symbol indicates a lower value for invasive species, and the '=' symbol indicates the invasive and non-invasive species had qualitatively the same response.

	'Rapid and profuse' strategy		'Bet-hedging' strategy	
Genus	Time to first germination	Proportion germinated	Germination period	Proportion dormant
Aristolochia	↓	=	↑	↑
Coreopsis	↓	=	=	↑
Genista	↓	=	↑	↑
Lonicera	↑	↓	=	↑
Passiflora	↓	=	↑	=
Salvia	↓	=	↓	=
Solanum	↑	↓	↑	↑

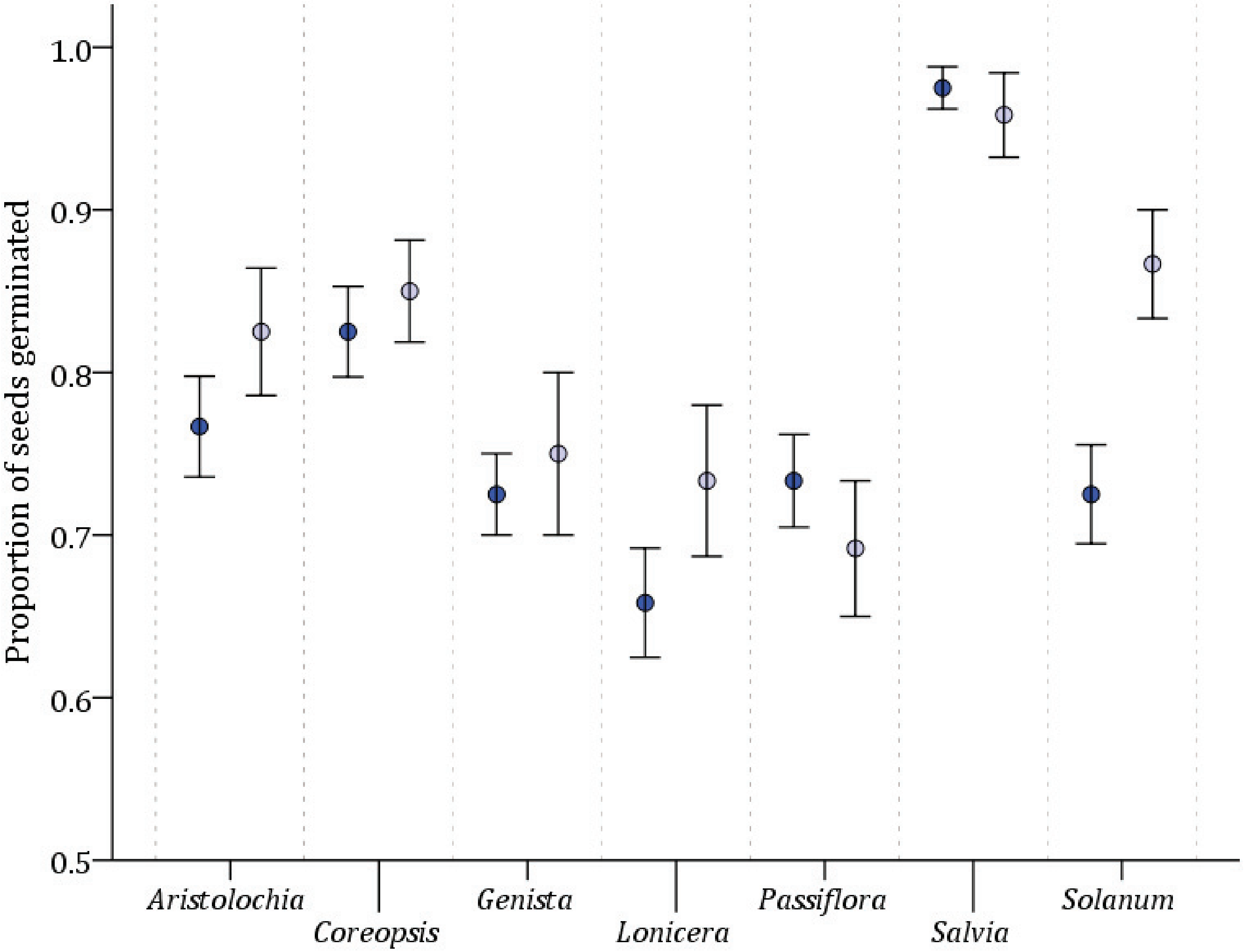

Figure 5.7. First germination (mean ± S.E.) compared across plant genera and as a function of invasiveness. Dark blue circles represent invasive species; light blue circles represent non-invasive species.

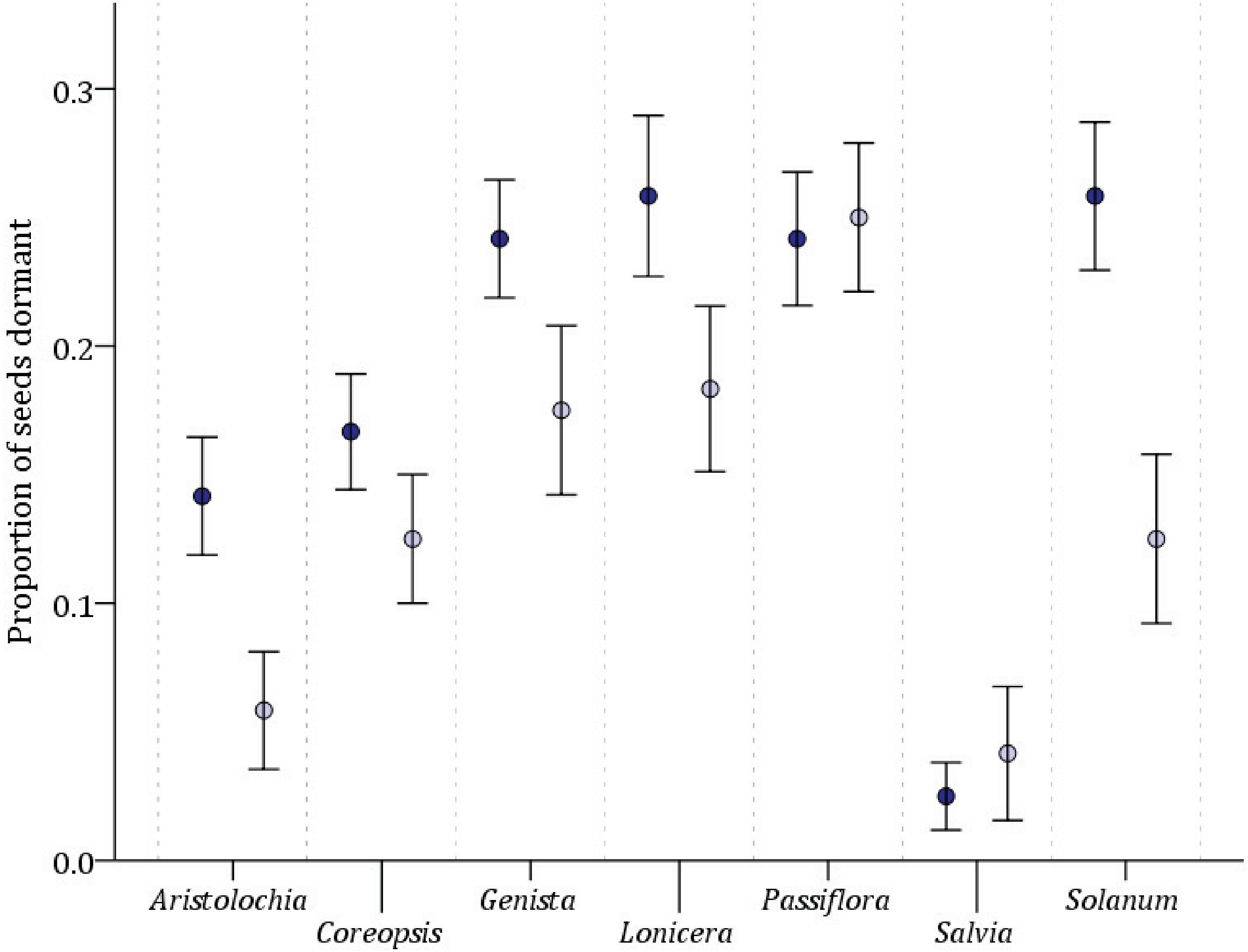

Figure 5.8. First germination (mean ± S.E.) compared across plant genera and as a function of invasiveness. Dark blue circles represent invasive species; light blue circles represent non-invasive species.

5.4 DISCUSSION

Using a moderately large number of congeneric species pairs representing contrasts of invasiveness across several different plant families, I found that invasive species were substantially more likely than non-invasive species to adopt a bet-hedging strategy for seed germination (Table 5.7). These findings provide support for predictions 2 and 4 (see Introduction). First, in four of the contrasts the invasive species staggered seed germination over a longer period of time than the non-invasive species during the experimental imbibition period. Second, the number of viable, ungerminated seeds at the end of the experiment (i.e. seed dormancy) was consistently higher in invasive than in non-invasive species for five of the seven congeneric contrasts.

Interestingly, three invasive species (*Aristolochia elegans*, *Genista monspessulana* and *Solanum torvum*) expressed bet-hedging through both staggered germination and increased seed dormancy. Previous work for Australia has shown that native plant species that delay germination via seed dormancy until the annual rain season arrives are more likely to survive and produce healthy seedlings than if their seeds germinate following an intermittent rainfall event outside the rain season (Turner *et al*. 2006, Bell *et al*. 2009). Given the patterns of sporadic rainfall events, heat waves and prolonged drought conditions within Australia, it is likely that staggered germination and increased seed dormancy may be a fundamental aspect to exotic species survival. From a management perspective, targeting the dormant seed bank of invasive species may become an increasingly important initiative in managing areas with well-established infestations of species. Promising new techniques are currently being designed and trialled for this purpose, including soil solarization which aims to eradicate infestations of some invasive species by depleting their persistent seed banks using heat transfer from polyethylene mulching (Cohen *et al*. 2008).

In three cases, the invasive species in the genera *Aristolochia*, *Coreopsis* and *Genista* all showed a rapid onset of germination followed by an increased investment in seed dormancy. In a study by Greenberg *et al*. (2001), an invasive woody vine introduced to North America, *Celastrus orbiculatus,* was found to exhibit a similar ‘sit and wait’ strategy. The species retained a viable dormant seed bank and responded to intermittent overstorey canopy disturbance with rapid (but not prolific) seed germination. Not unlike *C. orbiculatus*, both *G. monspessulana* and *A. elegans* are known to establish as understorey species and penetrate undisturbed natural environments, including woodland and forest areas, dense heathland vegetation and National Parks (Gillespie 1991, Carr *et al*. 1992, Skoien and Csurshes 2009). In the case of *C. lanceolata*, although typically an invader of disturbed edge habitats, the species has also been observed to encroach into undisturbed sclerophyll environments in the Blue Mountains region of New South Wales, Australia (*pers. obs.*). My results suggest an invasive strategy for invasive species that are capable of invading closed-canopy environments, whereby they invest in seed dormancy followed by a pulse of rapid germination to make the most of opportunities for increase in abundance. If the patterns I found for the genera in this study are repeated in other genera, this suggests that the power to predict species invasiveness based on germination traits could also, at least in part, be indicative of the habitat types in which the exotic species is likely to invade.

Intriguingly, the invasive herb *Salvia coccinea* did not display bet-hedging traits as predicted for invasives. *Salvia coccinea* did, however, exhibit a relatively short burst of seed germination, with germinants emerging within 2 days following moisture exposure. Given the high proportion of *S. coccinea* seeds that germinated throughout the course of this study (> 90%), there appear to be few seeds left to create a buffer against stochastic environmental hazards. Perhaps retaining a viable seed bank is less important if the seedlings of *S. coccinea* exhibit a high tolerance to environmental variation. In a study by Cervera and Parra-Tabla (2009), seed germination and seedling establishment traits of *Ruellia nudiflora*, an invasive species in Yucatan (Mexico) were compared with those of the congeneric non-invasive *R. pereducta*. Both proportion of seeds germinated and seedling survival rates were consistently higher for the invasive *Ruellia* compared to the non-invasive congener under high light conditions. The newly-developed seedlings of *R. nudiflora* exhibited significantly higher seedling survival through increased leaf-shedding (thus minimizing water loss) during drought conditions compared to the non-invasive congener (Cervera and Parra-Tabla 2009). Deeper exploration in to the life-history traits of *R. nudiflora* has found that the species does not retain a dormant seed bank and that seed viability decreases dramatically after 3 – 4 months (Abdala-Roberts *et al*. 2010). Given the relative fitness of invasive *R. nudiflora* seedlings, there appears to be little need for increased seed dormancy to endure periods of drought. Further investigation in to the seedling fitness of invasive *Salvia* species should uncover interesting patterns, especially in the context of seedling growth under environmental variation (see Chapter 6 of this thesis).

Across all plant genera, invasive species were consistently more likely to germinate much earlier than their non-invasive contrasts, with the exception of invasive *Lonicera* and *Solanum* shrub species, which went against this trend and germinated later. In a recent study by Wei *et al*. (2010), newly-ripened invasive *Solanum rostratum* required an extended period of darkness to reach maximum seed germination potential. One explanation for the lack of a consistent pattern in the *Solanum* pair in the present study is that some *Solanum* species might require longer periods of darkness beyond the period (24 hours) provided in this study and based on Hayati *et al*. (2005). Variation in the length and temperature of warm / cold stratification may also affect the germination of *Lonicera* species used in this study (Hidayati *et al*. 2000). Research which explores the impact of varying light and dark conditions on seed dormancy, as well as other factors including variation in ambient temperature, dormancy breaking techniques (such as extended stratification and gibberic acid) would be useful in unpacking this potential explanation.

Several *Lonicera* species are highly allelopathic, with plants producing chemical compounds that leach into the environment and have direct (or indirect) harmful or inhibiting effects on locally co-occurring plant species (Rice 1984) (e.g. *Lonicera japonica*; see: Skulman et al. 2004, *Lonicera mackii*; see: Dorning and Cipollini 2006). Importantly, however, the genus *Lonicera* is not known to be autotoxic, which is an intraspecific form of allelopathy that occurs when a plant species releases chemical substances that inhibit or delay the germination and growth of plants from its own species (Putnam 1985) (e.g. *Lonicera mackii,* Dorning and Cipollini 2006). Being allelopathic without being autotoxic may mean that once mature invasive *Lonicera* individuals have established within a new region, the pressure to germinate rapidly to compete with locally co-occurring species is less strong as the allelopathic influence of adult plants might be supressing the germination and growth of other species, thus facilitating a less-competitive transition from seed to seedling. Some previous studies have shown facilitation occurring between adults and seedlings (Pleasants and Jurik 1992, Roll *et al*. 1997, Montesinos *et al*. 2006), particularly in invasive (or 'weedy') species (McEvoy 1984, Wardle *et al*. 1991, Reinhart *et al*. 2006) and further exploration of this phenomenon for *Lonicera* species in Australia is merited.

For all four germination traits measured in this study, species' germination characteristics were intimately linked with taxonomic membership. Nevertheless, in addition to the taxonomic patterns, this study provides compelling evidence that within a genus, it is likely that invasive species are set apart from non-invasive species by a suite of life-history traits. For quarantine authorities, this would suggest an approach for management that compares traits of species considered for introduction with traits of already introduced species within the same genus if possible.

Having examined in detail comparative germination patterns in relation to invasiveness, in the next chapter I follow on the life-history path by investigating growth patterns in newly-established seedlings. I specifically test whether particular growth strategies might play an important role in driving plant species invasiveness beyond a successful germination strategy. How seeds that have successfully germinated grow and develop into seedlings under different soil moisture and nutrient conditions might provide valuable insights in to the invasion success of exotic species.

Chapter 6

Relationships between seedling traits and plant species invasiveness: a nutrient enrichment experiment

6.1 INTRODUCTION

The seedling stage is a perilous, transitional time for plants, with many species suffering an increased mortality rate during this life-history period (Harper 1977, Franklin *et al*. 1987, Peet and Christensen 1987, Oliver and Larson 1996). Seedling traits associated with comparatively better growth in new ranges may play a crucial role in promoting species invasiveness (Grotkopp and Rejmánek 2007, Morrison and Mauck 2007, Zheng *et al.* 2009, van Kleunen *et al.* 2010). Several studies that have assessed the importance of growth traits for species invasiveness have measured seedling traits within a single set of environmental conditions (e.g. Leicht-Young *et al.* 2007, Williams *et al*. 2008, Berg and Ellers 2010). This common-garden approach is extremely valuable in providing a 'level playing field' in which to observe trait relationships with invasiveness for one or more species under benign or favourable conditions. What this approach cannot assess, however, is how plant growth traits respond to a shift in environmental conditions and how this might be linked to species invasiveness (Burns 2004).

A common observation about invasive plant species is that many are capable of growing profusely across a broad spectrum of environmental conditions (Elton 1958, Baker 1965, Sultan 2001, Daehler 2003, Pigliucci 2005, Rejmánek *et al*. 2005). In particular, there is field-based evidence that invasive plant species thrive in disturbed habitats where there is nutrient enrichment, such as on the edges of native vegetation (e.g. Li and Norland 2001, King and Buckney 2002, Lake and Leishman 2004, Zimmerman *et al*. 2007). Experimentally, a recent study (Skálová *et al*. 2012) found that seedlings of invasive species within the genus *Impatiens* produced consistently higher biomass compared with less-invasive species across a range of manipulated soil nutrient conditions. Interestingly, this seedling response was also found to be highly plastic, with species biomass shifting two-fold in the invasive species in response to high nutrient conditions. At present, however, there have been no studies exploring the

importance of growth traits for species invasiveness that have used congeneric pairs of invasive and non-invasive species from across a range of plant taxonomic families.
In this chapter, relationships between seedling growth traits and plant species invasiveness were assessed using four congeneric pairings of invasive and non-invasive species. In a glasshouse experiment, I compared the species' performances within these pairings between soil nutrient conditions typical of Sydney bushland (NSW, Australia) and soil conditions representing high nutrient enrichment typical of disturbed edge habitats of vegetation in the Sydney region, where the species in each congeneric pairing are known to co-occur. Manipulating soil conditions and observing the response of co-occurring congeners in this way may give clear patterns as to how some species are able to respond to altered soil nutrient conditions and become invasive while other closely-related species do not.

The aim of this study was to test predictions about a suite of growth traits and their possible role in facilitating invasiveness. The traits included time to seedling emergence as well as seedling height, leaf production, specific leaf area and plant biomass at the end of a three month experimental period. Broadly speaking, seedlings of exotic plant species that can emerge from the soil faster and demonstrate better (i.e. more competitive) growth characteristics (including increased height, higher leaf production, higher specific leaf area and larger biomass) will be more likely to establish and become invasive compared with species with slower emergence and poorer growth. I tested the following specific predictions linking interspecific variation in seedling growth traits to species invasiveness:

(i) The seedlings of invasive species will emerge from the soil faster than the seedlings of non-invasive species;

(ii) The seedlings of invasive species will be taller than the seedlings of non-invasive species, and more so under nutrient-enriched conditions;

(iii) The seedlings of invasive species will have more leaves than the seedlings of non-invasive species, and more so under nutrient-enriched conditions;

(iv) The seedlings of invasive species will have higher specific leaf area compared to the seedlings of non-invasive species, and more so under nutrient-enriched conditions;

(v) The seedlings of invasive species will acquire larger biomass than the seedlings of non-invasive species, and more so under nutrient-enriched conditions;

6.2 METHODS

6.2.1 GLASSHOUSE EXPERIMENT

Congeneric pairs were selected using the species selection framework outlined in Chapter 3 and based on the availability of fresh seed. Pairs of invasive and non-invasive species from the genera *Coreopsis*, *Paspalum*, *Passiflora*, and *Salvia* were used in this study (Table 1). Three other pairs were also tested (*Solanum*, *Lonicera* and *Genista*) but unfortunately there were insufficient numbers of emergent seedlings at the time of the experiment for one or both species of each pair to be included for experimental purposes.

Fresh seed of each of the study species was sourced from field populations or commercial seed suppliers from three naturalised populations within Australia. For each species, four lots of 50 seeds were weighed (to µg precision on a LIBROR-AEL-160 electronic analytical balance, Shimadzu, Japan) and mean seed mass was calculated. Seed mass was measured prior to the experiment as the seed coat plus embryo and endosperm, with all dispersal structures removed prior to weighing (Table 6.1 shows the similar mean seed mass of the two species in each congeneric pair). Using the same methodology as Chapter 5, a squeeze test was performed on seeds for all species. All viable seeds used in the experiment were surface sterilized by inundating seeds in a 10% solution of sodium hypochlorite (NaOCl) for fifteen minutes to remove any potential pre-existing pathogenic contamination that could affect the germination rates of seeds in the experiment.

Table 6.1. Invasive and non-invasive exotic plant species in each of the four congeneric contrasts used in this study.

Genus	Species	Family	Status	Growth form	Longevity	Mean seed mass (mg)
Coreopsis	*Lanceolata*	Asteraceae	Invasive	Herb	Perennial	2.693
Coreopsis	*Grandiflora*	Asteraceae	Non-invasive	Herb	Perennial	2.279
Paspalum	*Dilatatum*	Poaceae	Invasive	Grass	Perennial	0.846
Paspalum	*fragrantissima*	Poaceae	Non-invasive	Grass	Perennial	0.986
Passiflora	*Foetida*	Passifloraceae	Invasive	Vine	Perennial	8.344
Passiflora	*Coccinea*	Passifloraceae	Non-invasive	Vine	Perennial	7.832
Salvia	*Coccinea*	Lamiaceae	Invasive	Herb	Perennial	2.063
Salvia	*Splendens*	Lamiaceae	Non-invasive	Herb	Perennial	4.421

Seeds of all species were pre-treated to break dormancy at varying times using different methods (as reported in Chapter 4) to ensure that seeds were at a similar stage of maturity at the time of planting. Both the invasive and non-invasive *Paspalum* species were found to germinate readily and therefore were only soaked for 6 hours prior to sewing.

Viable pre-treated seeds were sewn into pots at a depth of 10 mm, a measurement standardised via the use of a small hollow tube with markings on the outside. In each pot six seeds were buried, evenly spaced, to allow for potential seed mortality (as reported in Chapter 4) or prolonged dormancy (as reported in Chapter 5) without reducing the number of experimental replicates (pots). Although seeds were pre-treated to break dormancy, seeds were not pre-germinated (i.e. planted after radicle and cotyledon emergence had occurred) as I was interested in measuring seedling emergence (as a result of seed germination in the soil) as a response to variation in soil conditions.

Pots measuring 95 mm width x 95 mm length by 125 mm depth were filled with sandy, low-nutrient potting soil (i.e. 'Native Low P mix', a low phosphorus native mix blended from soil, coarse sand and composted sawdust; Australian Native Landscapes PTY LTD, Terrey Hills NSW). Native Low P mix was selected for use in the study due to its closeness to natural soil conditions in many parts of bushland New South Wales, Australia (i.e. sandy, low soil nutrients) and availability in large quantities. Hawkesbury Sandstone soils of the Sydney region, for instance, have markedly low phosphorus concentrations (typically 30 to 80 mg kg^{-1}; Beadle 1962) compared to elsewhere in the world (e.g. UK average 650mg kg^{-1}, USA average of 500 mg kg^{-1}; Williams and Raupach 1983), while soil nitrogen concentrations can vary from 180 to 600 mg kg^{-1} (Hannon 1956). Before the experiment began, the soil was sterilised by spreading it on flat, heat-proof trays and placing the trays in an oven at 80°C for 1 hour. This process was to eliminate any pathogens and insects that may have been present without adding any chemical pesticides or fungicides which may have altered the soil conditions (McCall 1981). The sterilised soil was coarsely sieved and large chunks of wood and bark were removed to ensure the soil in each replicate pot was uniform. The batches of dry soil were then mixed together in a large container to minimise the likelihood of soils from any particular tray being different and confounding seedling growth patterns. Nutrient analyses of the soil were compared with soil samples taken from bushland region in the

Sydney region and N, P and K contents were within the typical ranges of Hawkesbury Sandstone soils of the Sydney region (M. Phillips, unpub. data).

Pots were arranged in a temperature-controlled glasshouse at the University of Technology Sydney during December 2010 and monitored daily for 4 weeks, then four times a week for the following 8 weeks. If more than one seedling emerged from a pot, the surplus seedlings were gently extracted using round-point tweezers, removing all plant parts with minimal disturbance to the soil. The glasshouse had nylon shade cloth fitted to the ceiling and main sun-facing wall, providing approximately 50% shading to the seedlings throughout the study. The shade cloth remained closed to prevent excessive heat build-up in the air, and in addition, glasshouse vents automatically opened to release warm air if the air temperature exceeded 28° C. Maximum and minimum temperatures in the glasshouse during this time were logged by the *Priva Integra* glasshouse system (Priva Agro BV, De Lier, The Netherlands) as 32.8° C and 16.5° C, respectively. Throughout the course of the study period there was no indication of toxicity or salt build-up in the soil. The glasshouse ceiling was fitted with strips of insect-attracting sticky paper which were changed weekly to eliminate the potential for insect activity. I found no evidence of herbivore damage (e.g. chewed holes or degraded tissue) on any of the seedling leaves during the experiment.

Seedlings were allocated to one of two treatments (control or nutrient enrichment) with 8 replicate seedlings per treatment of each of the eight species. Both the control and nutrient enrichment treatment were watered twice per week with approximately 200 mL of pure water per pot in order to provide soil moisture saturation with minimal water leakage out of the base. No extra nutrients were added to the control pots. The nutrient enrichment treatment was designed to increase nutrient availability to levels consistent with soils receiving nutrient-rich stormwater runoff (e.g. adjacent to urban creeks or below stormwater outlets at the residential/bushland interface). At every alternate watering event, approximately 4 ml of complete fertiliser was added to the water given to seedlings in each nutrient-enriched replicate (N:P:K concentration – 10.5:2.3:6.8; Nitrosol™, Ecofertiliser Pty Ltd., Stapylton, Queensland, Australia).

Pots for each species and treatment were randomly arranged across four benches in the glasshouse. Pots were cycled within benches four times a week and across benches twice a week. The treatments were continued for three months before final seedling measurements were taken.

6.2.2 SEEDLING MEASUREMENTS

I monitored pots in the glasshouse every two days for the first 4 weeks and measured the time from seed sewing to seedling emergence for each species following the method described by van Kleunen and Johnson (2007). At the end of the 12 week period, I recorded leaf production by counting the number of expanded leaves present on each seedling. I determined the height of each seedling (to the nearest mm) by measuring the distance from the soil layer to the height of apical meristem in dicotyledonous species, and to the end of the longest leaf in *Paspalum* monocotyledonous species.

Using protocols described in *PrometheusWiki* (an open communication wiki for protocols, methods, explanations and updated standards in ecological and environmental plant physiology; see Sack *et al*. 2010), a fresh, undamaged leaf was scanned for each seedling replicate using a flatbed scanner on the same day as the seedling was harvested; all petioles and sheaths were removed prior to scanning. Leaf area was calculated from the scanned leaves using Image J software (Rasband 2006, Davidson and *Prometheuswiki* contributors 2012). Following scanning, I dried the leaves in an oven set at 60° C for three days and then weighed each dried leaf individually to calculate specific leaf area (i.e. fresh leaf area (cm^2) per unit of dry leaf weight (g)) (Cornelissen *et al*. 2003), in between measurements storing the dry leaves in large sealed Ziploc™ bags filled with a tablespoon of dry silica desiccant. Seedlings were placed in labelled paper bags and oven-dried at 60°C for three days in order to calculate biomass accumulated (g), making sure to add the mass of dried specific leaf area leaves as well as removed petioles and sheaths in the total biomass calculation.

6.2.3 STATISTICAL ANALYSES

The seedling trait data were assessed for normality by performing a series of One-Sample Kolmogorov-Smirnov (K-S) tests in SPSS Statistics (SPSS Inc, version 20, IBM). The K-S tests revealed the majority of seedling traits were not normally distributed ($P < 0.001$) and could not be transformed to improve normality, thereby violating a key assumption of parametric tests. Furthermore, pilot analyses showed that there was significant heterogeneity of variances among the treatments for all of the seedling traits. The use of generalized linear models in place of general linear models was inappropriate in this situation given that no error structure and link function could be specified to account for the nature of the seedling trait data. As a result, an analytical strategy that was different to the previous chapters had to be adopted. Each genus was analysed separately, for each of the five seedling traits which were treated as separate response variables. By comparing seedling traits between the invasive and non-invasive species in each genus separately, I was able to avoid the use of non-normal data and to maintain homogeneity of variances for all statistical tests. General linear mixed models (SPSS Inc., version 20, IBM) were used with invasive status (invasive, non-invasive) and nutrient enrichment (control, enriched) as fixed predictor variables and genus as a random variable. A significant effect of status would indicate that invasive and non-invasive species differed in the mean values of the relevant growth trait. A significant effect of nutrient enrichment would mean that plants differed in the mean values of the relevant growth trait between the control and enriched groups. Importantly, a significant interaction between status and nutrient enrichment, with invasive species responding more favourably under the nutrient enrichment treatment, would mean that invasive species exhibit greater performance plasticity (e.g. Burns 2004, Pohlman *et al*. 2005).

6.3 RESULTS

6.3.1 Time to seedling emergence

Seedlings of the invasive herb species *Coreopsis lanceolata* emerged earlier from the soil compared with seedlings of non-invasive *C. grandiflora* (Table 6.2, Fig. 6.1). This pattern was consistent with the 'time to first germination' patterns reported for *Coreopsis* species in Chapter 5. I found no other link to earlier seedling emergence for invasive seedlings or any significant effect of nutrient enrichment on time to seedling emergence for any of the other species pairs.

Table 6.2. General linear models relating seedling emergence and growth traits (along the first row of the table) to invasive status and soil nutrient enrichment separately within each congeneric pair. 'Interaction' is that between invasive status and soil nutrient enrichment.

Genus	**Source**	**Time to emergence**			**Seedling height**			**Leaf production**			**Specific leaf area**			**Seedling biomass**		
		F	d.f.	*P*	F	d.f.	*P*	F	d.f.	*P*	F	d.f.	*P*	F	d.f.	*P*
Coreopsis	Status	5.108	1	**0.032**	0.057	1	0.813	0.392	1	0.537	0.078	1	0.782	2.722	1	0.110
	Nutrients	0.007	1	0.934	18.113	1	**<0.001**	9.790	1	**0.004**	90.260	1	**<0.001**	34.110	1	**<0.001**
	Interaction	0.343	1	0.563	0.442	1	0.512	0.881	1	0.356	0.867	1	0.360	1.706	1	0.202
Paspalum	Status	1.532	1	0.226	0.047	1	0.830	0.009	1	0.924	0.111	1	0.742	0.052	1	0.821
	Nutrients	0.681	1	0.416	6.540	1	**0.016**	0.232	1	0.634	28.629	1	**<0.001**	12.649	1	**0.001**
	Interaction	0.043	1	0.838	1.164	1	0.290	0.751	1	0.394	0.635	1	0.432	2.100	1	0.158
Passiflora	Status	0.003	1	0.956	5.015	1	**0.033**	0.051	1	0.822	0.807	1	0.377	0.009	1	0.924
	Nutrients	0.374	1	0.546	68.186	1	**<0.001**	6.205	1	**0.019**	8.263	1	**0.008**	173.361	1	**<0.001**
	Interaction	0.003	1	0.954	6.411	1	**0.017**	0.205	1	0.654	2.350	1	0.136	1.130	1	0.297
Salvia	Status	0.367	1	0.549	0.002	1	0.961	0.668	1	0.421	7.520	1	**0.011**	0.160	1	0.692
	Nutrients	1.469	1	0.236	79.142	1	**<0.001**	2.383	1	0.134	26.439	1	**<0.001**	94.755	1	**<0.001**
	Interaction	0.041	1	0.841	0.723	1	0.402	0.008	1	0.928	0.170	1	0.683	2.952	1	0.097

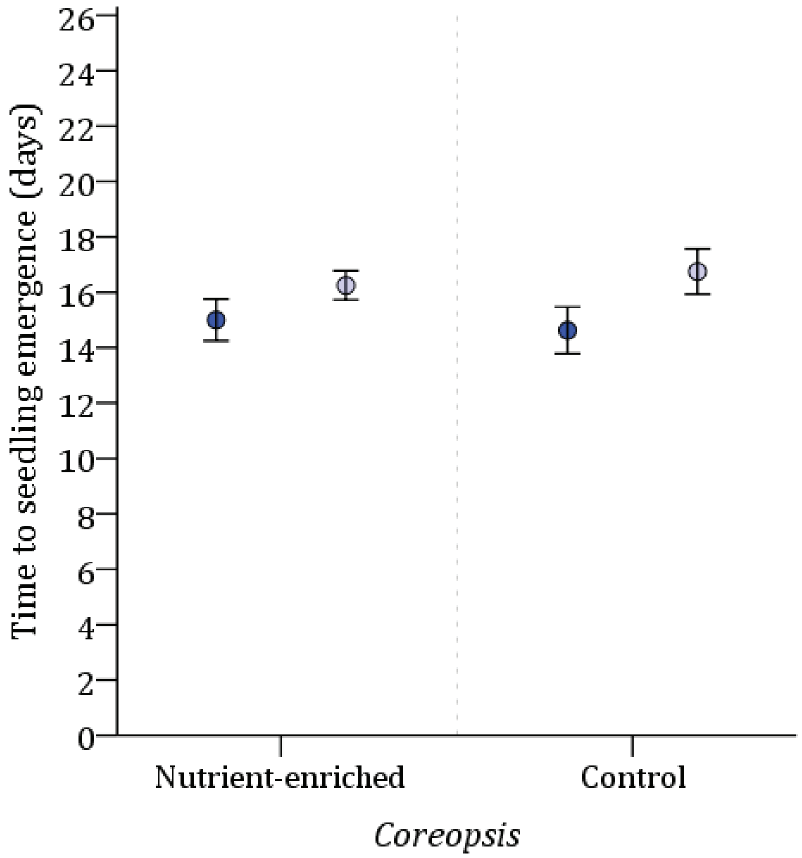

Figure 6.1. Time to seedling emergence (mean ± S.E.) of *Coreopsis* seedlings compared across nutrient conditions and as a function of invasiveness. Dark blue circles represent the invasive *Coreopsis lanceolata* which had a shorter time to emergence; light blue circles represent the non-invasive *C. grandiflora*.

6.3.2 Seedling height at 12 weeks

Seedlings of the invasive vine *Passiflora foetida* were significantly taller than those of *P. coccinea* seedlings at 12 weeks (Fig. 6.2), a pattern which supports my second prediction. Interestingly, a significant interaction between species invasiveness and nutrient enrichment for seedling height was detected in *Passiflora*. Invasive *P. foetida* seedlings were the same average height as the non-invasive *P. coccinea* seedlings under high nutrient conditions, but under low nutrient conditions, the invasive *P. foetida* seedlings were slightly taller than the non-invasive congener. Within all other congeneric pairs, seedlings of both invasive and non-invasive species grew significantly taller with soil nutrient enrichment (Table 6.2).

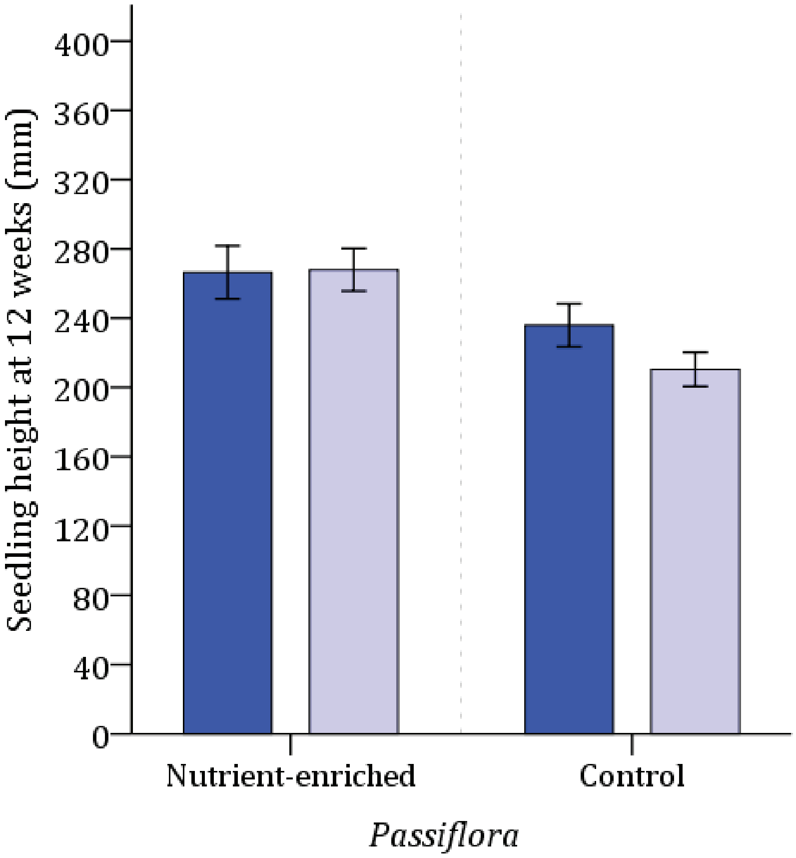

Figure 6.2. Seedling height (mean ± S.E.) of *Passiflora* seedlings at 12 weeks compared across nutrient conditions and as a function of invasiveness. Dark blue circles represent invasive *Passiflora foetida*; light blue circles represent non-invasive *P. coccinea*.

6.3.3 Leaf production after 12 weeks

The seedlings of invasive species did not produce more leaves than their non-invasive congeners in any of the congeneric pairs (Table 6.2). Leaf production for seedlings of *Coreopsis* and *Passiflora* species increased significantly with nutrient enrichment, but not for *Paspalum* or *Salvia* species (Table 6.2).

6.3.4 Specific leaf area

Seedlings of the invasive herb *Salvia coccinea* had higher SLA than the seedlings of non-invasive *S. splendens* (Table 6.2, Fig. 6.3). No statistical interaction was detected, indicating this difference was consistent for *Salvia* species across nutrient enriched and control soil conditions. Specific leaf area was not significantly linked to invasiveness in the genera *Coreopsis*, *Paspalum* or *Passiflora*. Specific leaf area was consistently and significantly higher in soil nutrient enrichment conditions compared with control pots for seedlings of all species (Table 6.2).

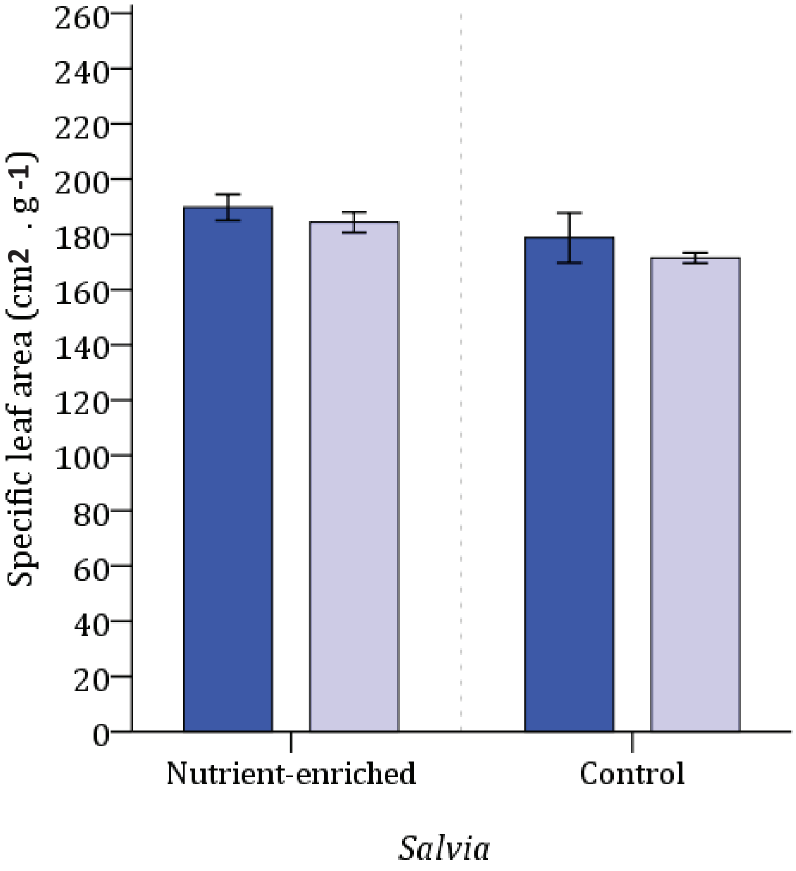

Figure 6.3. Specific leaf area (mean ± S.E.) of *Salvia* seedlings compared across nutrient conditions and as a function of invasiveness. Dark blue circles represent invasive *Salvia coccinea*; light blue circles represent non-invasive *S. splendens*.

6.3.5 Biomass

Overall, I found that the seedlings of invasive species did not accumulate significantly larger biomass than congeneric non-invasive species. Biomass was significantly larger in soil nutrient enrichment conditions compared with control pots for the seedlings of all species (Table 6.2).

6.4 DISCUSSION

Using congeneric species pairs representing contrasts of invasiveness across different plant families, I found no consistent link between species invasiveness and either seedling emergence or early growth traits. I did, however, uncover some evidence that invasive species can emerge from the soil earlier (e.g. *Coreopsis*) or grow taller under low nutrient conditions (e.g. *Passiflora*) or produce higher specific leaf area (e.g. *Salvia*) compared with non-invasive species, but these patterns were not consistent across all invasive species. In addition, I found that plant growth of exotic species can be significantly enhanced by soil nutrient enrichment, providing evidence that disturbed, nutrient-enriched edge habitats enhance seedling growth of exotic plant species which underscores the susceptibility of disturbed native vegetation to exotic species incursions.

Rapid seedling emergence is a trait that has been previously linked to increasing the likelihood of naturalisation among groups of related species. In a study by van Kleunen and Johnson (2007), seedling emergence and growth were explored using 30 congeneric pairings of naturalised and casual South-African *Iridaceae* species with the aim of determining whether seedling traits increased the likelihood of naturalisation success. While seed mass did not differ between naturalised and casual *Iridaceae* species, the naturalised species consistently emerged faster from the soil and, as a consequence, reached a larger seedling size earlier than the non-naturalised species. My study shows a similar trend for *Coreopsis* seedlings; the invasive species consistently emerged faster from the soil than the congeneric non-invasive species despite having the same average seed masses, although this earlier emergence did not promote increased seedling height, biomass accumulation or leaf production over the non-invasive congener. Nevertheless, earlier emergence would provide a competitive advantage over other non-invasive exotic plant species. *Coreopsis lanceolata* is a ruderal species that often forms dense, monoculture infestations of plants that reproduce both clonally and sexually; each plant at reproductive maturity is capable of generating hundreds of seeds per reproductive event (M. Phillips, unpublished data). Efficient germination followed by rapid and consistent seedling emergence, as expressed by *C. lanceolata*, may be promoting the monoculture type of invasive spread that the species exhibits.

It is interesting to note that invasive *Salvia* and *Passiflora* species found to germinate 1 – 3 days earlier in the previous chapter emerged from the soil about the same time as their non-invasive congeners under the experimental conditions. Seed germination and seedling emergence are complex plant functions and their rate of occurrence is likely to be influenced by a large number of factors, including soil warmth and sunlight. Deeper investigation of the influence that abiotic conditions (besides soil nutrients) play in modifying the germination and emergence of these particular invasive species could unearth important insights for weed managers and policy makers alike.

Leaf traits play a central role in carbon assimilation, as well as plant hydrological and energy balance. High specific leaf area is among a suite of leaf attributes (also including high photosynthetic capacity, high foliar nitrogen and short leaf lifespan, Reich *et al*. 1997) that is associated with vigorous plant growth. Specific leaf area is also a trait that separates exotic species from co-occurring natives across a range of habitat types (Pattison *et al*. 1998, Durand and Goldstein 2001, Smith and Knapp 2001, Grotkopp *et al*. 2002). This pattern could indicate that fast growth under non-limiting conditions (e.g. nutrient-plentiful soils) may be contributing to the invasion success of some exotic species. Research over the last ten years exploring this idea has linked increased specific leaf area to species invasiveness (e.g. Grotkopp *et al*. 2002, Burns 2004, Lake and Leishman 2004, Grotkopp and Rejmánek 2005, Burns 2006, van Kleunen *et al*. 2009), although Leishman and Thompson (2005) found that this pattern may not be a consistent predictor of species invasiveness for exotic plant species in Australia. In my study, the invasive *Salvia coccinea* did have significantly higher specific leaf area compared to the non-invasive congener *S. splendens*. The other invasive species, however, expressed similar specific leaf areas to their non-invasive counterparts. I suggest that specific leaf area may be a context-specific predictor of species invasiveness, whereby some species retain a fast growth advantage over others, whereas others do not. I have shown in Chapter 5 that, unlike some invasive species, *S. coccinea* does not appear to retain a dormant seed bank. Therefore the increased seedling specific leaf area for this species may be an indicator of increased seedling fitness (Cervera and Parra-Tabla 2009), thus negating the species' need to maintain a viable seed bank in order to bet-hedge against shifting environmental conditions (see Chapter 5).

Specific leaf area has been consistently shown to increase significantly for many species in conditions of increased soil nutrient availability (Hamann 1979, Dolph and Dilcher 1980, Givnish 1984, Skarpe 1996, Cunningham *et al*. 1999, Fonseca *et al*. 2000, Nicotra *et al*. 2007). My study results are consistent with this global pattern; seedlings of both the invasive and non-invasive species had higher specific leaf area following soil nutrient enrichment, as well as increased biomass and seedling height.

The invasive vine species, *Passiflora foetida,* grew slightly taller than non-invasive *P. coccinea* at low-nutrient soil conditions. This pattern could indicate that seedling height of *P. coccinea* is nutrient-limited. It also shows that under 'control' soil conditions (e.g. undisturbed Sydney bushland) the invasive *P. foetida* demonstrates a growth 'edge' over the non-invasive *P. coccinea*. A recent study investigating early growth traits of *Passiflora* species linked seedling emergence and growth to sun-exposure, with seedlings of multiple *Passiflora* species growing significantly taller, as well as gaining higher specific leaf area and biomass accumulation under increased sun exposures (Pires *et al*. 2012). Sun exposure in my study was limited to 50% cover, a feature which is likely to have affected the seedling growth of open canopy species including *Passiflora* (as well as *Paspalum dilatatum* which can grow to 1 m tall, and *P. fasciculatum* which can grow as high as 3 m tall). Therefore, I suggest a future study could explore the emergence and growth attributes of related invasive and non-invasive species under a range of sun exposures. I also observed some invasive species (e.g. *Salvia coccinea*), although not taller than the non-invasive counterpart, did appear to sprawl outwards more. Measuring the sprawling canopy effect some species exhibit could give an indicator of competitive ability over other locally co-occurring species.

Accumulating larger plant biomass indicates a faster uptake of resources and more efficient conversion of resources into plant matter. Previous research within the one genus has identified increased biomass accumulation as an indicator of species invasiveness (e.g. Skálová et al. 2012), but this trend was not evident in my study species. Increased leaf production and biomass accumulation were also not found to be linked to invasiveness in my study species. Considering all of these results together, it seems likely that seedling emergence and growth traits will not emerge as consistent predictors of invasiveness across plant taxa.

It is worth noting that although I used seeds from three different naturalised populations within the introduced range of each species, I did not explore any within-species population differences as factors that might promote competitive seedling growth in invasive vs. non-invasive species. Recent research has found that variation in phenotypic plasticity among different populations of the same species may be a major source of trait variation (e.g. Nicotra *et al*. 2007). Knight and Ackerly (2003), for instance, reported significant differences in the specific leaf areas of coastal and desert *Salvia* species in a complementary field and common glasshouse study. The authors observed significant within-species shifts in specific leaf area when comparing plants grown in the field to those in the common garden glasshouse; specific leaf area increased up to 24% in the glasshouse environment. Accounting for within-species differences in plant traits as well as across species variation may be the next step in comparative studies of plant invasiveness in the future. Utilising a complementary glasshouse and field study would be a desirable step in determining whether the emergence and growth patterns of invasive and non-invasive species are consistent under additional pressures of environmental variation, co-occurring competitors, herbivores and soil biota. I note here that it is relatively easy to locate naturalised populations of invasive exotic plant species in Australia, but due to their limited geographic distributions, finding multiple naturalised populations of co-occurring contrasted non-invasives is a much more difficult task.

Chapter 7

Plant species of the Central European flora as exotics in Australia

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7.1 INTRODUCTION

Exotic species are nowadays widespread and there is virtually no region of the world free of invasive plants (Pyšek *et al*. 2008). Exotic plant species invade a wide range of habitats (Stohlgren *et al*. 1999, 2006, Chytrý *et al*. 2005, 2008a, b, 2009a, b, Lambdon *et al*. 2008, Pyšek *et al*. 2010a, b), exert serious ecological impacts on invaded ecosystems (Parker *et al*. 1999, Mack *et al*. 2000, McGeoch *et al*. 2010, Vilà *et al*. 2010), incur huge costs to economies (Perrings *et al*. 2000, Pimentel *et al*. 2005, Binimelis *et al*. 2007, Kettunen *et al*. 2009, Vilà *et al*. 2010) and are subject of management efforts (see Pyšek and Richardson 2010 for a review). The distribution of invasive species on continents (Weber 2003), which shapes current global patterns of plant invasions (Lonsdale 1999, Pyšek *et al*. 2008), is a result of historical factors (di Castri 1989), differences in vulnerability of regions to invasion (Lonsdale 1999), opportunistic human-induced dispersal via various introduction pathways (Hulme *et al*. 2008, Hulme 2009) and interactions with native biota in regions of introduction (e.g. Richardson *et al*. 2000a, Sax and Gaines 2008, Vilà *et al*. 2009,Walther *et al*. 2009, Winter *et al.* 2009, Schweiger *et al*. 2010).

Historically, the exchange of exotic biota between continents has not been random, reflecting factors such as cultural background, intensity of trade and movement of human populations (di Castri 1989, Thuiller *et al*. 2005). Successful translocation of plant and animal species from one continent to another also reflects the climatic match between the target and source region (Panetta and Mitchell 1991, Rouget *et al*. 2004, Thuiller *et al.* 2005, Bomford *et al.* 2009). As such, the geographic origin of an exotic species is an important trait that has been shown to play a role in the temporal sequence of arrivals into target regions (Kowarik 1995, Pyšek *et al.* 2003) and in predicting a species ability to naturalise (Pyšek *et al.* 2009b).

In contrast to most studies that focus on exotic floras of target regions (the 'target-area' approach, see Pyšek and Richardson 2007 for a review), a 'source-area' approach has been developed (Prinzing *et al.* 2002, Pyšek *et al.* 2004b, 2009a), which means that the invasiveness of species in the introduced range can be explored by considering the complete species pool of a specific source region. This partly minimizes some of the biases associated with propagule pressure (e.g. distance to source areas) and evolutionary predispositions acquired in various regions of origin. It is based on the assumption that members of the flora of a single biogeographical region have comparable chances to be transported by humans from their native region to other parts of the world. Thus, the structure of an exotic flora that they form can be more unequivocally attributed to their traits, because biases related to different chances of species being translocated from the source pool are reduced (Pyšek *et al.* 2009a). For example, it may be easier for species to be translocated to the introduced range from a closer source region than from one that is more distant. The advantages of the source-area approach remain valid even though many species were not introduced from the source region directly to the target region, but may have reached it via another region on the donor continent to which they were introduced at an earlier time (LaSorte and Pyšek 2009). In the present paper, I use such an approach to explore the source pool of Central European plant species as exotic species in Australia, thus linking a region on a continent that historically acted as a major donor of exotic species to other parts of the world (di Castri 1989, Pyšek 1998) with the one that is among the most seriously affected by invasions globally (Randall 2007). The Old World, Europe and Western Asia have served as an important donor area of exotic species to other regions of the globe (di Castri 1989) and European species in particular have experienced many centuries of testing their invasion potential in a wide range of conditions.

European colonists permanently settled in Australia in 1788, originally established by the British as a penal colony. Since colonial establishment at the end of the 18th century, a total of 26,242 plant species have been introduced to Australia (Randall 2007). A comparatively small number of these introduced species may have arrived in Australia, predominantly in the remote northern regions of the continent, several years before as a result of trading by native Aborigines with peoples of southeast Asia (Groves *et al*. 2005). Over all this time, many different regions of the world have donated exotic plant species to Australia including Asia, South America, North America, Africa and Europe (Groves and Hosking 1998, Cook and Dias 2006, Harris *et al*. 2007, Phillips *et al.* 2010).

Unlike in Europe, where the patterns and history of plant invasions have been the focus of enormous research effort, enabled by a detailed knowledge of regional and continental exotic floras (e.g. Kühn and Klotz 2003, Pyšek *et al*. 2003, 2005, Křivánek and Pyšek 2006, Chytrý *et al*. 2008b, 2009a, Lambdon *et al*. 2008, Hulme *et al.* 2009, Štajerová *et al*. 2009, Knapp *et al*. 2010, Kubešová *et al*. 2010, Pyšek *et al*. 2010a, c), there is a comparative paucity of information concerning such patterns and processes for Australia. While a growing body of disparate work over the last 20 years is beginning to raise the profile of the importance of understanding patterns and processes in exotic plant introductions for Australian ecosystems (e.g. Lonsdale 1994, Groves and Hosking 1998, Lake and Leishman 2004, Hamilton *et al*. 2005, Leishman *et al*. 2007, Murray and Phillips 2010, Phillips *et al*. 2010), we are far from possessing as comprehensive an understanding of exotic plant introductions to Australia as has been developed for some other regions of the world.

Exploration of temporal patterns of introduction of exotic plant species to different regions of the world can provide important baseline information in the study of large-scale patterns of introduction and naturalisation (e.g. Fuentes *et al.* 2008). For instance, if it can be determined that there were influxes of exotic plant species, families or life histories during particular periods of human population growth and expansion, it becomes possible to understand more fully the introduction to naturalisation transition in exotic plants in relation to patterns of human exploration (e.g. colonization of new continents), technological advances (e.g. more rapid movement of humans around the globe via air travel), agricultural development (e.g. introduction of pasture species) and societal events (e.g. world wars or economic cycles). If these temporal patterns of introduction can also be considered in regard to the current status of exotic species in new regions (e.g. whether the species have become naturalised or not), then we can start to understand the role of shifting patterns of human activity through time in facilitating the introduction to naturalisation pathway and subsequent plant invasion. This study explores historical patterns of introduction of exotic plant species to Australia.

Specifically, this study focuses on exotic plant species in Australia in relation to the large source pool of species of Central Europe.

This study examined temporal patterns of species introduction to Australia across the Central European species source pool and explore relationships between introduction time and (i) method of introduction (deliberate or accidental), (ii) current status of species (casual or naturalised), (iii) plant taxonomy (family) and (iv) plant growth form. This study is the first component of a larger investigation into the introduction-history, life-history and ecological factors underpinning naturalisation and invasion success among Central European plant species in Australia. Importantly, it is through our deepening comprehension of patterns of historical introductions to Australia that we may better understand why some species are more successful than others at becoming naturalised and why other plant species are unable to sustain established populations within Australia.

7.2 MATERIALS AND METHODS

7.2.1 Source species pool

The flora of the Czech Republic (Kubát *et al.* 2002) and Germany (Klotz *et al*. 2002) was taken as a source species pool to obtain a sample of plant species that are native to Central Europe and belong to the Central European floristic element (Oberdorfer 2001). This approach is justified by the geographical location of these countries in the centre of the continent and by both having one of the strongest floristic traditions among European countries. The earliest accounts of the complete flora of the territory of the Czech Republic date from the beginning of the 19th century (see Pyšek *et al.* 2002 for an overview), and there is a recently compiled modern national flora (Hejný and Slavík 1988–1992, Slavík 1995–2000, Slavík and Štěpánková 2004) and identification key (Kubát *et al.* 2002). Scientific floristic inventories in Germany date back to 1687 (Knauth 1687, see Knapp *et al*. 2010 for details) with the first floras of large parts of the current German territory dating back to the early 19th century (Röhling *et al.* 1823–1839, Garcke 1849, 1871). Modern distribution atlases (Haeupler and Schönfelder 1989, Benkert *et al.* 1998) were compiled into databases and are regularly updated (www.floraweb.de). The most recent complete checklists are from Wisskirchen and Haeupler (1998) and Buttler and Hand (2008). In addition, there is very good knowledge on the traits of species occurring in these two regions (Kühn *et al.* 2003, 2004, 2006, Klimešová and Klimeš 2008, Küster *et al.* 2008, 2010), their distribution across different habitats (Sádlo *et al.* 2007) and affiliation to vegetation units inferred from large databases (e.g. Douda 2008, Schaminée *et al.* 2009, Dúbravková *et al.* 2010)

For the Czech Republic, the compilation of the dataset followed the procedure described in Pyšek *et al.* (2009a), using the working database *CzechFlor* held at the Institute of Botany, Průhonice, and the same criteria were applied to compiling data from Germany, using the *BIOLFLOR* database (Klotz *et al.* 2002). This screening yielded 1845 vascular plant species of Central European distribution occurring in the Czech Republic and/or Germany. These species are a highly representative sample as illustrated by comparison of their commonness/rarity in the region compared with pan-European patterns. Species frequencies in the Czech Republic and Germany, expressed as the number of ca 11 × 12 km grid cells from which a species has been reported, are highly correlated in frequency ($r = 0.85$, d.f. = 1154, $P < 0.001$) and very well reflect species frequency in the digitized *Atlas Florae Europaeae* (see www.fmnh.helsinki.fi/english/botany/afe and references therein; $r = 0.89$, d.f. = 313, $P < 0.0001$, for Czech and German species from the study data set combined for which European distribution data are available). *Atlas Florae Europaeae* is currently only available for ca 20% of European species; however, it is a highly representative sample showing that the frequencies in the Czech Republic and Germany are well able to serve as proxies for the size of a species' native European range. For that reason, I term the species identified as using the above criteria as the “Central European source species pool”.

Since the native range has been shown to affect the probability that a species will be introduced to other regions of the world (Pyšek *et al.* 2009a), this correlation allows the assumption that the chances of species in the Central European source species pool being introduced elsewhere also reflect their chances of being introduced from Europe as a whole.

7.2.2 Target region data

The Central European source species pool list was compared with a recent comprehensive database of all known plant introductions to Australia (Randall 2007) to extract the set of Central European species that have been recorded in Australia. Of the 26,000 exotic species introduced to Australia, 759 plant species were of Central

European origin (species nomenclature followed Randall 2007). The present study does not infer that Central European plant species in Australia were transported directly between the two regions. Indeed, it is likely that many of the species arrived namely via Britain, given its historical association with Australia, and also other parts of the world. Nevertheless, this factor does not invalidate this investigation, as (i) the focus in this study is specifically on providing an analysis of the contemporary source pool of Central European plant species in Australia in relation to general patterns of introduction history, and (ii) there is a close correlation between the distribution of the source pool species in Central Europe and in Europe as a whole, including the UK (see above).

I accessed the Australian Census of Cultivated Plants 2009 database from the Department of Agriculture, Fisheries and Forestry (DAFF) and obtained data on both the earliest year of introduction of the species to Australia as well as the means by which the species arrived in Australia. For the purposes of this research, earliest year of introduction refers to the earliest known record of a species being imported to, or reported within, the country. Method of introduction was divided into two categories, deliberate (e.g. species known to be brought in as ornamental or garden plants) or accidental (no known purposeful reason for introduction), as this was the most detailed information available for the species in the dataset. Public domain sources including over 600 plant nursery catalogues spanning 200 years, botanical and major garden plant species lists, Australian Quarantine and Inspection Service (AQIS) permitted import list, State department vegetation surveys and Commonwealth lists of imported species have been meticulously sourced for the DAFF database (R. Ingram, personal communication).

Information on taxonomic membership, at the level of family, and the current status of each species in Australia (casual or naturalised, corresponding to definitions in Richardson *et al.* 2000b, Pyšek *et al*. 2004a) was obtained from Randall (2007). In the present study, cultivated species that may have escaped from cultivation and that have not become naturalised are considered casual species. The data available do not allow the consistent discrimination between cultivated and non-cultivated species that occur as casuals in the Australia flora; hence they are pooled into a single meaningful category. Each species in the database was classified according to its growth form as (i) tree, (ii) shrub, (iii) herb or (iv) grass with data on growth forms sourced from *CzechFlor*, a working database of national flora held at the Institute of Botany, Průhonice, which was compiled using the monographs of national flora (Hejný and Slavík 1988–1992, Slavík 1995–2000, Kubát *et al*. 2002, Slavík and Štěpánková 2004) and other sources. Herbs included all herbaceous species with the exception of grasses. Species in the *Cyperaceae* and *Juncaceae* were considered as herbs.

7.2.3 Statistical analysis

A χ^2 contingency table analysis (i.e. analysis of independence in a two-way table, Quinn and Keough 2002) was used to test for differences in the number of species among categories that included naturalised accidental, naturalised deliberate, casual accidental and casual deliberate introductions. In addition, standardized residuals (differences between the observed and expected values) from the analysis were determined to illustrate the direction of patterns emerging from contingency analysis. To compare frequency distributions of introduction times between different categories (e.g. accidental vs. deliberate introductions) non-parametric Kolmogorov-Smirnov tests were used.

7.3 RESULTS

7.3.1 Central European species in Australia: a summary

Across all species, substantially larger numbers of species were introduced between 1840 and 1880 as well as between 1980 and the present, with a small peak of introductions within the 1930s (Fig. 7.1). The majority of species had deliberate (69%) rather than accidental (31%) introductions and most species have not become naturalised (66% casual species, 34% naturalised species). Interestingly, significantly more naturalised (but fewer casual) species than expected were introduced accidentally rather than deliberately (χ^2 d.f. = 1 = 551.96, $P < 0.0001$, standardized residuals: accidental naturalised = 15.92, deliberate naturalised = –10.57, accidental casual = –11.33, deliberate casual = 7.60). The earliest record of an accidental introduction was in 1802 for *Daucus carota* which is now a naturalised species, while the earliest record of a deliberately introduced species was in 1803 for the casual species *Corylus avellana*. In total, 86 different plant families comprising 31 tree species, 91 shrub species, 533 herbaceous species and 61 grass species present in Central Europe have been introduced to Australia.

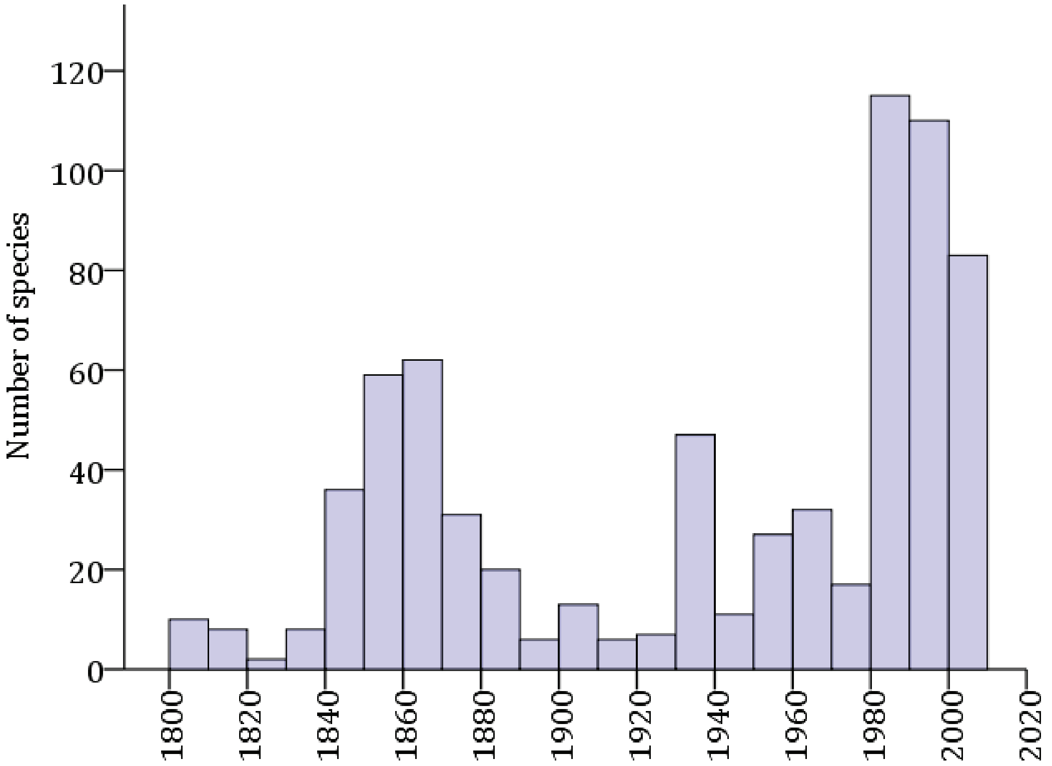
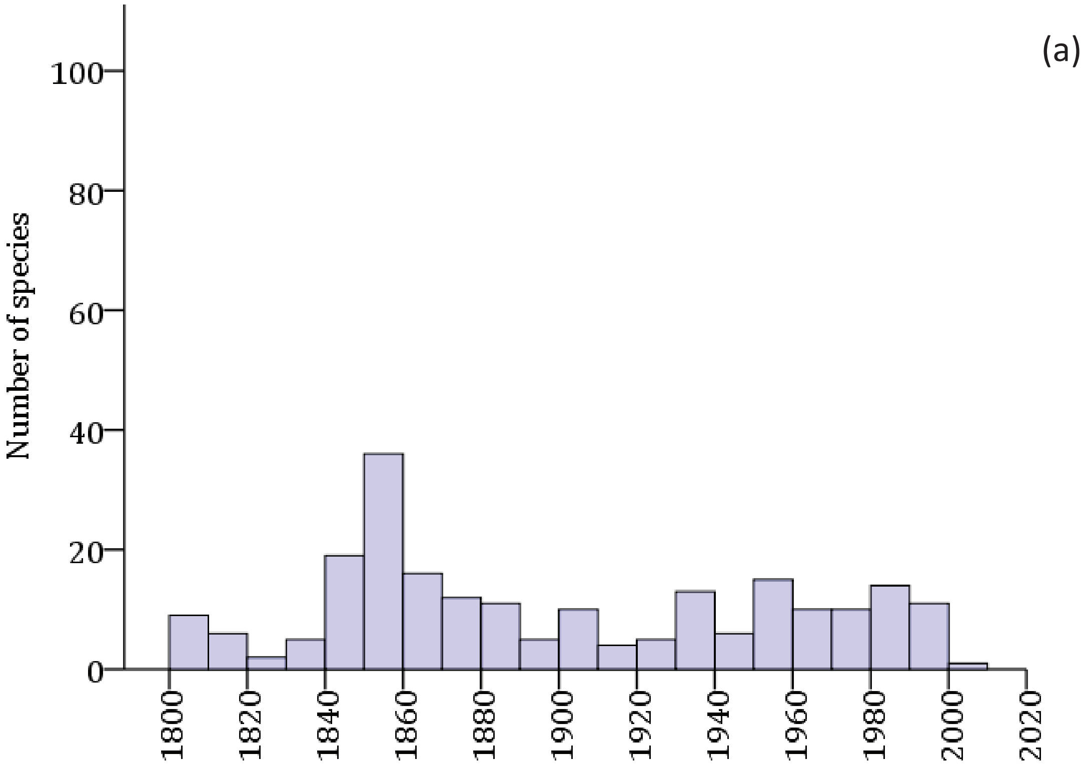


Figure. 7.1. Frequency distribution of introduction times for all Central European plant species that have been introduced to Australia.

7.3.2 Accidental and deliberate introductions over time

Examination of temporal patterns of introduction as a function of method of introduction (accidental or deliberate) revealed that the high peak of recent introductions was largely due to a substantial increase in deliberate introductions since the early 1980s (Fig. 7.2). There was a significant difference in frequency distributions of introduction times between species arriving accidentally and deliberately (Kolmogorov-Smirnov test: $Z = 11.33$, $P < 0.0001$). The spike in introductions observed during the 1930s was a product of considerably more deliberate introductions compared with accidental introductions, while the second highest peak in introductions, from 1840 to 1880, appears to have been generated by similarly large numbers of accidental and deliberate introductions during this time.



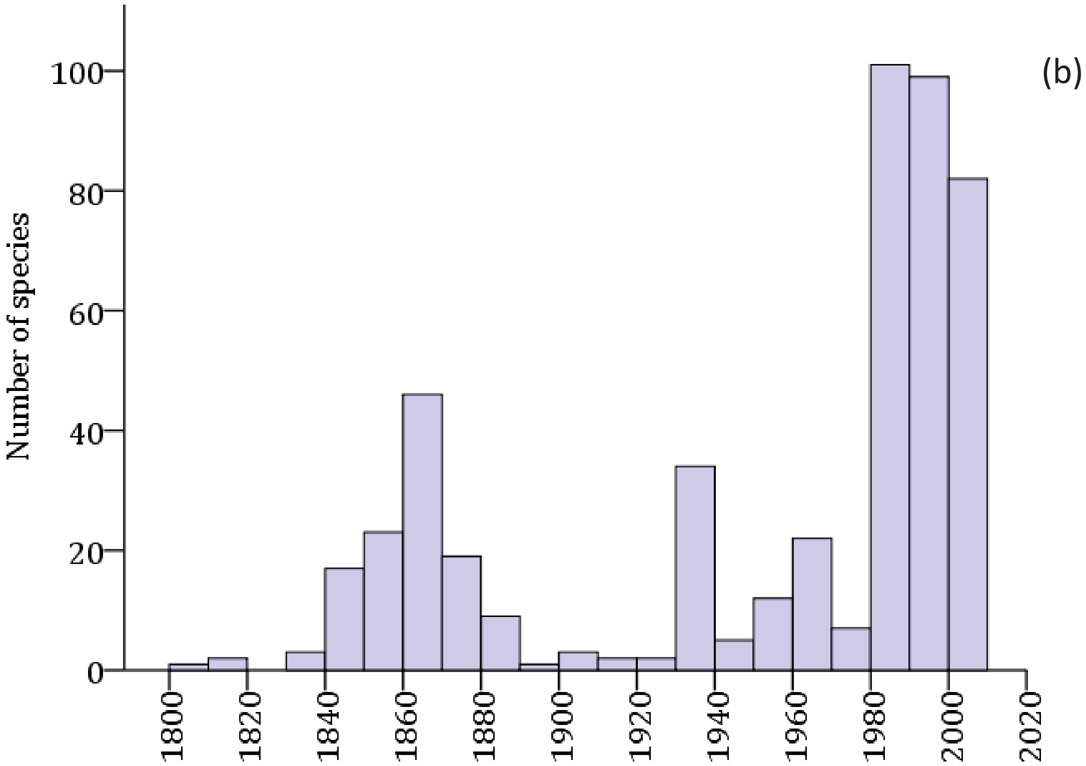


Figure. 7.2. Frequency distributions of introduction times for species that were introduced (a) accidentally or (b) deliberately.

7.3.3 Current status of Central European plants in Australia in relation to introduction periods

Consideration of temporal patterns of introduction as a function of the current status of species (casual and naturalised species, Fig. 7.3) showed that the peak of recent introductions (i.e. since the 1980s) can be linked to larger numbers of casual than naturalised species. Indeed, there was a significant difference in frequency distributions of introductions between casual and naturalised species (Kolmogorov-Smirnov test: $Z = 6.12$, $P < 0.0001$). It is worth noting, however, that the large number of species with introductions between 1840 and 1880 appears to be made up of equivalent numbers of casual and naturalised species.

7.3.4 Introductions of plant families over time

Three major groups of plant introduction emerged by examining temporal patterns of introduction as a function of plant family (Fig. 7.4 illustrates patterns of introduction times for the 13 most speciose families, represented by more than 15 species). First, most species from several of the larger plant families (*Apiaceae, Brassicaceae, Campanulaceae, Cyperaceae, Lamiaceae* and *Scrophulariaceae*) were introduced quite recently (since the 1960s). Second, most species from two families (*Poaceae* and *Fabaceae*) were introduced in the more distant past (between the late 1800s and the late 1920s). Third, other families (*Asteraceae, Caryophyllaceae, Ranunculaceae, Rosaceae* and *Salicaceae*) reveal a long and consistent pattern of species' introductions to Australia.

7.3.5 Introductions of plant growth forms over time

The temporal breakdown of species' introductions as a function of growth form revealed intriguing patterns of variation (Fig. 7.5). Tree species were introduced mostly in the mid-1800s with many fewer trees arriving since then. Grass species similarly appear to have been restricted in their introductions, mostly to earlier periods in Australia's history of colonization, while herbs and shrubs have had a long and consistent pattern of species' introductions to Australia since the mid to late 1800s.

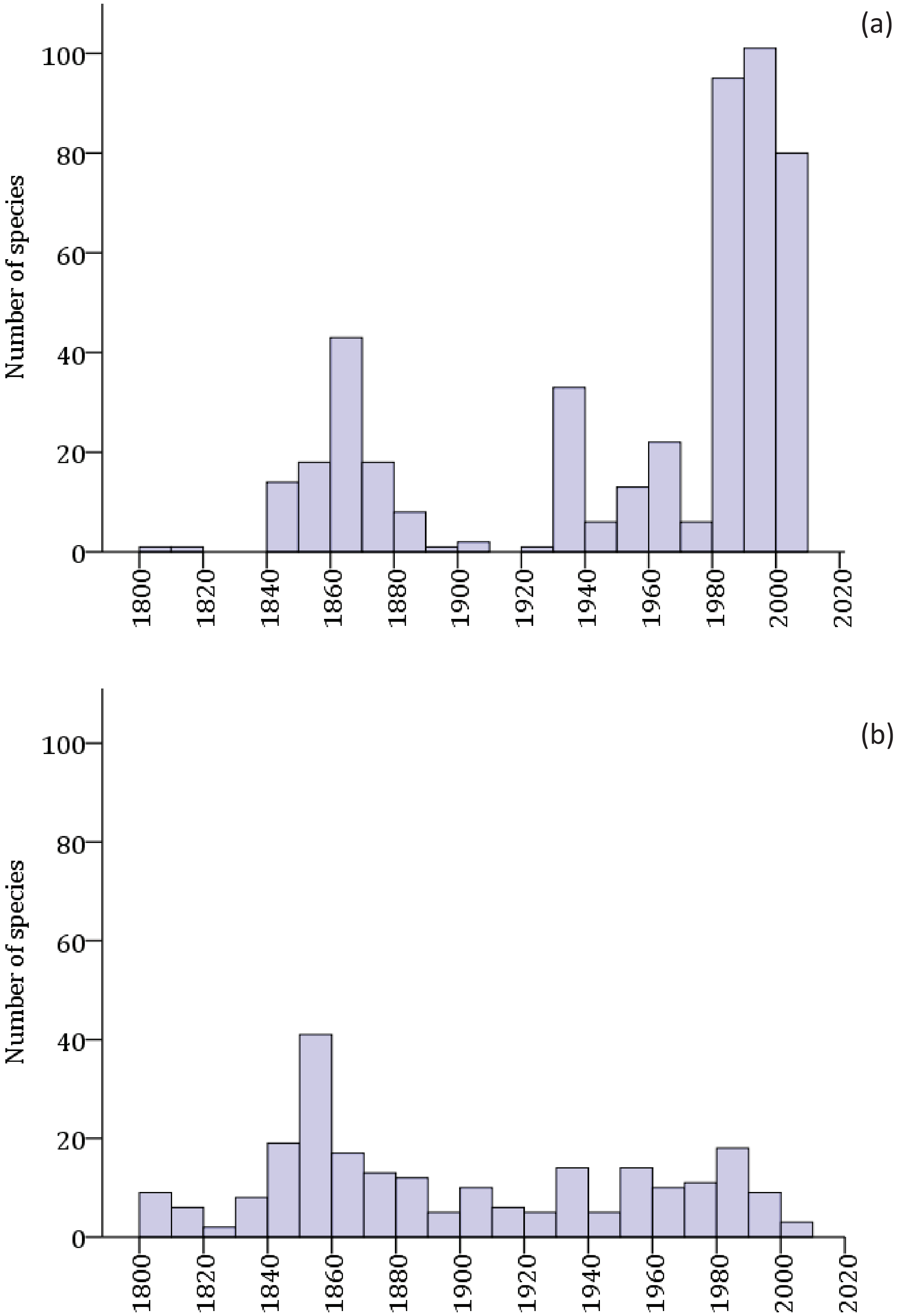


Figure 7.3. Frequency distributions of introduction times for species that are currently classed as (a) casual or (b) naturalised.

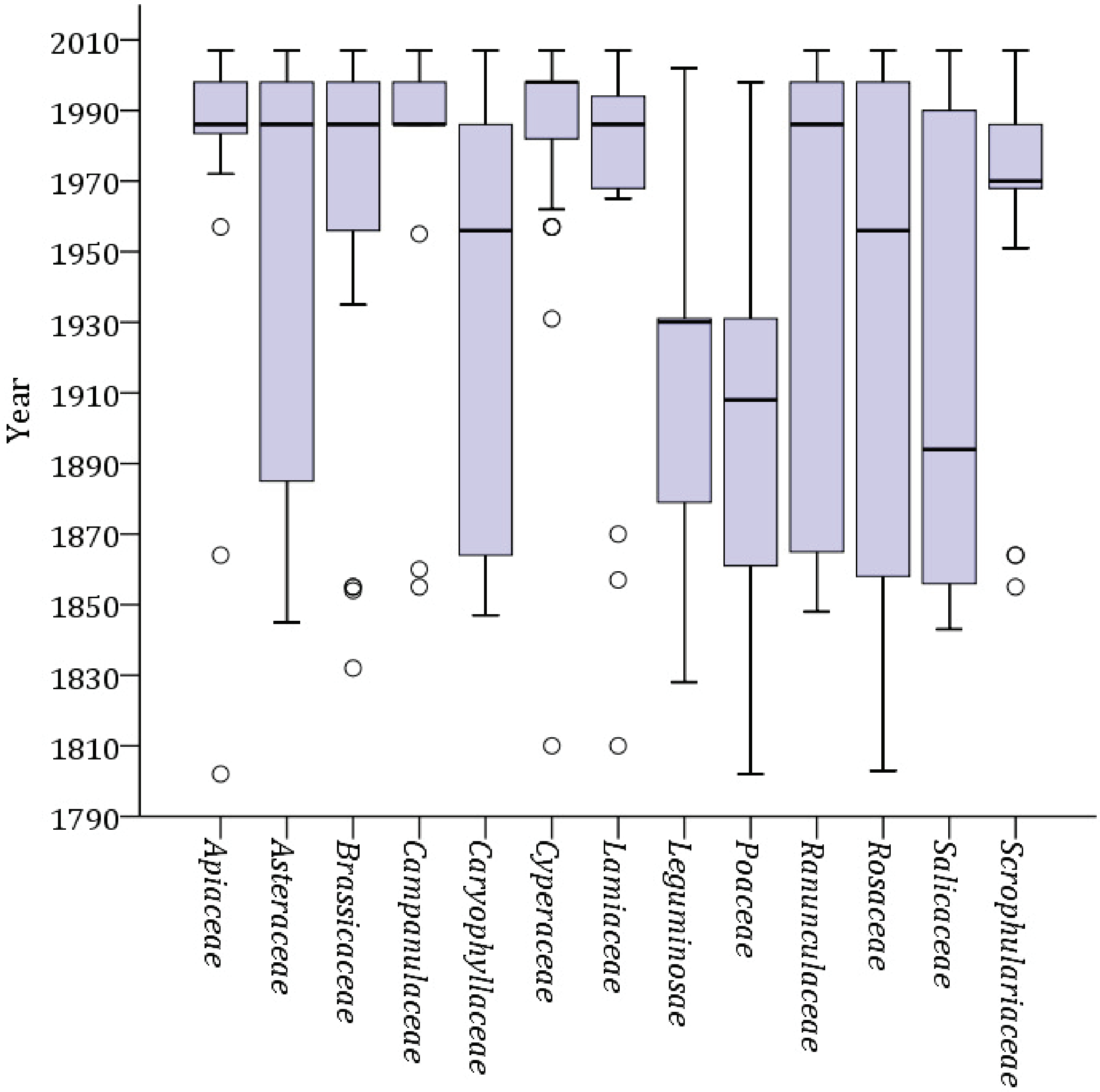


Figure 7.4. Distribution of earliest years of introduction for families with more than 15 species. The median, upper and lower quartile, smallest and largest non-outlier observations and outliers are presented. Outliers are those further away than 1.5 times the interquartile range (box).

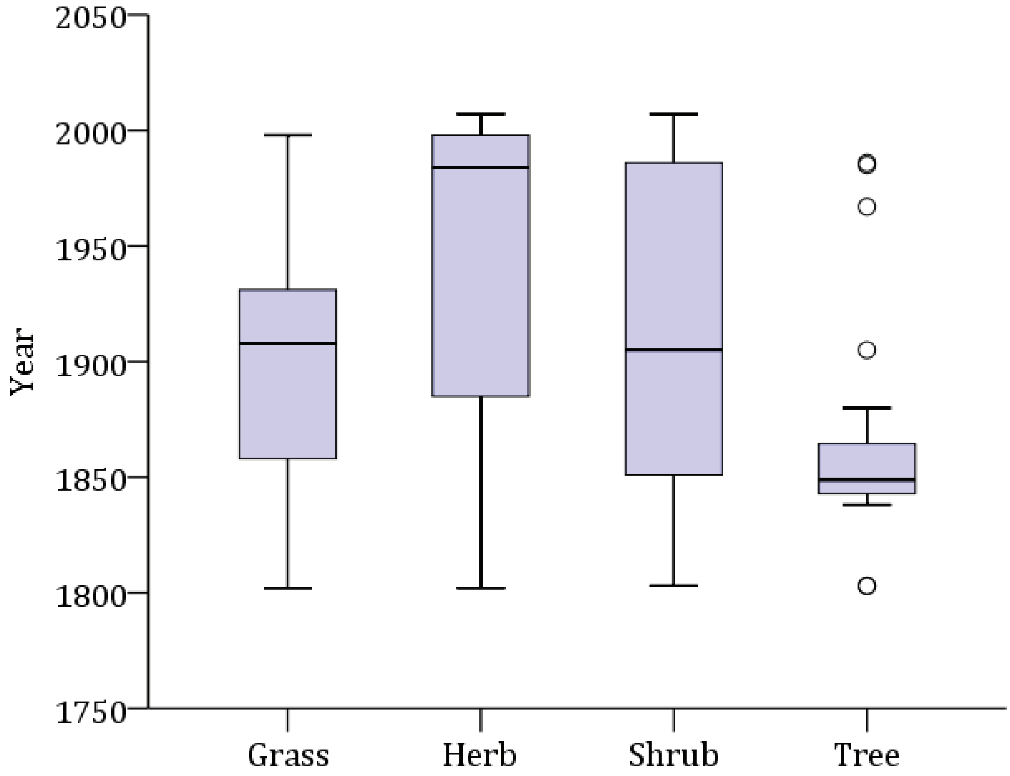


Figure 7.5. Distribution of earliest years of introduction for species in each of the four plant growth forms. The median, upper and lower quartile, smallest and largest non-outlier observations and outliers are presented. Outliers are those further away than 1.5 times the interquartile range (box).

7.4 DISCUSSION

The results reveal two peak periods of introduction among the source pool of Central European plant species in Australia. The first peak occurred between 1840 and 1880 and the second peak between 1980 and 2000. There was also a smaller rise in introductions during the 1930s.

The first major influx of species coincides with convict transportation to Australia during the first half of the 19th century. During this time, transportation became the preferred punishment for crime over the death penalty in Britain and Ireland, and over 100,000 convicts were sent to Australia before 1840 (Sherrington 1980). An additional 58,000 free colonial settlers emigrated from the United Kingdom to Australia between 1815 and 1840, as the promotion of affordable settlement and lifestyle became a new driving force behind migration to Australia (Sherrington 1980).

These social changes were then followed by the 'Gold Rush', beginning in 1851 with the discovery of gold near the township of Bathurst in New South Wales. The Gold Rush stimulated a large increase in foreign immigration to Australia as migrant families, primarily from the United Kingdom, continental Europe and Asia, sought wealth through gold prospecting and the establishment of businesses to support the new gold mining industry (Bligh 1973, Sherrington 1980). Census data from 1851 report the Australian colonial population was approximately 437,655, but by the end of the decade it had increased over two-fold to 1,151,947 (Sherrington 1980).

As human migration to Australia became more frequent, so followed the movement of commodities and possessions, including seeds and plants that were introduced both intentionally (e.g. orchard species) and unintentionally (i.e. through contamination of grain) (Groves *et al*. 2005). Migrant families that travelled to Australia to establish a new lifestyle often sought to make their properties and gardens reflect the aesthetics of their countries in order to preserve their unique cultural identities (Sherrington 1980). In 1848, the first retail botanical nursery was opened in Sydney, after which the nursery and horticulture trades developed continuously within Australia (Bligh 1973). Exotic plants became a common feature of new gardens, in the first instance with many gardening societies being formed along with botanical gardens that often displayed ornamental specimen plants from many parts of the world, including popular tree species like European ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*), both introduced from Central Europe and both grown and sold commercially in Australia during the 1850s (Shepherd 1851, Macarthur 1857, Pembroke 2009).

The second significant peak period of plant introductions (occurring during the 1980s to 2000s) follows the rapid development of communications and transport networks in Australia. In addition, there appears to have been a rise in the popularity of gardening culture in Australia through the medium of television. Following this, exotic ornamental species have become valuable aesthetic commodities to Australian gardeners, with many publications and websites promoting the use of ornamental exotic plants as desirable features within garden settings. The number of new plant species, including species already invasive in Australia, that are able to be legally imported into States and Territories of Australia is extremely large (Glanznig 2005). Some 162,000 plant species are able to be legally imported into all States and

Territories (except Western Australia) with no risk assessment, which is about 60% of all vascular plant species on Earth (Whitton and Rajakaruna 2001).

Interestingly, this trend of recent increase in plant introductions to Australia contrasts with findings for New Zealand, where rates of plant introductions and naturalisations are in decline (Williamson *et al.* 2010). Despite carefully elaborated protocols of Australian weed risk-assessment and intensive research in this field (Pheloung *et al.* 1999, Gordon *et al.* 2008, 2010, Weber *et al.* 2009) plant introductions continue to increase. The ease with which an exotic ornamental species may be ordered and brought into Australia through the postal system is often noted as highly problematic for their control, despite Australian Quarantine's rigorous screening systems to detect and prevent the entry of unauthorized exotic plant species (Ernst and Young 2007). It has been recently reported that the collaborative efforts of Australian Quarantine and Australia Post have had considerable difficulty meeting targets and effectiveness benchmarks for screening international mail and large container cargo (i.e. to detect biological material such as seeds), especially in Western Australia, and have consistently failed to meet mail screening targets during the Christmas holiday period when the volume of international mail and importation to Australia peaks annually (Ernst and Young 2007). These failures in the biological screening protocol present open opportunities for exotic species to be imported to Australia without permit (Australian Biosecurity Group 2005, Ernst and Young 2007).

The third peak of plant introductions that occurred during the 1930s was of smaller magnitude and appears to be isolated within a smaller period of time, in contrast to the longer duration of the two main plant introduction peaks. This may be accounted for by the pre-war immigration of Central European citizens to Australia during the 1930s. Prior to World War II, there was a large expatriation of European families as a result of the rising political tensions and outbursts of violence in European countries, with Australia receiving approximately 170,529 British immigrants in the 1920s and into the 1930s (Sherrington 1980). This would also coincide with a large number of immigrants coming to Australia because of economic difficulties during the Great Depression of 1929–1933. The majority of species had deliberate rather than accidental introductions. One possible explanation for this pattern is that there has been a botanical recording bias. In other words, it is perhaps far easier to keep records of species' introductions if species have been brought in purposefully, than to record accidental introductions across a large area such as Australia. However, there is some evidence that deliberate introductions do perhaps comprise the majority of introduction events. The gardening industry is by far the largest importer of introduced plant species, being the source for the introduction of 25,360 or 94% of new plant species into Australia and garden plant introductions are also the dominant source of new naturalised plants and weeds in Australia; in fact, of the 2779 introduced plant species that have naturalised in the Australian environment, 1831 (or 66%) are escaped garden plant species (Groves *et al*. 2005). This is comparable to the situation in Europe where the majority of species have been introduced deliberately for ornamental or horticultural reasons (Lambdon *et al.* 2008, Pyšek *et al.* 2009c) and the more widespread a species is, the higher its frequency in botanic gardens (Hanspach *et al*. 2008). This is probably also reflected in the pattern of introduction of different growth forms over time (Pyšek *et al.* 2003). Tree species to provide building material, shelter, shadow and some sort of "home feeling" in the new settlements were brought to Australia rather early, as many European migrant families desired familiar plant species that reflected their traditional cultures (Bligh 1973). Grasses followed soon after, mainly for agricultural reasons (pastures), although some grasses are also prone to accidental introduction, for example, due to their awns sticking to clothes (Groves *et al.* 2005). More recently, gardening and ornamentation were responsible for the vast numbers of shrubs and herbs introduced to Australia (Groves and Hosking 1998, Groves 2005).

Several European plant species have become commonplace within Australia since their early introductions. The earliest known intentional introduction is the common hazel (*Corylus avellana*) brought in to Australia as a nursery plant in 1803. Common hazel is a tall, deciduous shrub or small tree with multiple human uses, the most notable use being the production of edible nuts; it is also able to grow as a hedgerow species and its timber can be harvested for fence posts. Norway maple (*Acer platanoides*) was introduced from Europe in 1843. Landscape designers frequently use Norway maple as an avenue tree to line city streets for a more "traditional" street aesthetic. Heal-all (*Prunella vulgaris*), introduced in 1810, is both an edible and medicinal herb used for its antibacterial properties. All parts of the plant are used for a variety of alternative medicinal treatments, including teas, soups and salads.

The peak of recent (i.e. after 1980) introductions to Australia is made up largely of species currently classed as casual species. This is probably a reflection of their short residence time in their new range. An invasion ecology generality is that long residence time is correlated with a wide distribution and invasiveness (Rejmánek 2000, Castro *et al.* 2005, Pyšek and Jarošík 2005, Harris *et al.* 2007,Wilson *et al.* 2007,Williamson *et al.* 2009, Gassó *et al.* 2010, Phillips *et al*. 2010). Although much less studied, residence time is also most likely correlated with a species likelihood of becoming naturalised (Pyšek and Jarošík 2005, Křivánek *et al.* 2006). It is quite a daunting prospect then, that with so many casual species entering the continent, there is a strong likelihood that we shall see many more exotic plants becoming naturalised and potentially becoming serious invaders to rival Australia's current worst invaders, due to their still running lag times (Kowarik 1995).

Chapter 8

Synthesis

8.1 THESIS OVERVIEW

The introduction of exotic plant species into new regions is one of the main drivers of global change, causing major disruptions to ecosystem processes and functioning (Vitousek *et al*. 1997, Mooney and Hobbs 2000), in addition to widespread biodiversity and economic losses (Pimentel *et al*. 2005, Sax and Gaines 2008). The sheer magnitude of scale at which this change occurs underscores the need for exploring new methods that accurately discriminate which exotic plant species, once introduced, will become invasive. Scientists continue to investigate many aspects of the ecology, biology and physiology of invasive species in order to fulfil this task, attempting to answer perhaps the most fundamental question in invasive species research: 'what are the characteristics of exotic plant species that lead to invasion success?' This is a complex question to unravel and to effectively answer this question we must apply the sharpest ecological 'tools' we have in our toolkit.

Previous studies have sought to identify plant traits that predict species invasiveness (e.g. Baker 1965, 1972, Booth *et al*. 2003). Some scientists have put forward the argument that this is not an achievable task (e.g. Roy 1990, Alpert and Simms 2002), and some have even written of their disappointment with trait-based predictive research altogether (Moles *et al*. 2008). I believe that this is a serious misinterpretation of previous work. Indeed, Rejmánek (1996) argued cogently that plant traits are a crucial ingredient for explaining and strong contenders for predicting plant species invasiveness. Since then, research has shown, by the use of sophisticated multi–species comparisons, that successful invasive species do have important trait commonalities (e.g. Goodwin *et al*. 1999, Cadotte and Lovett-Doust 2001, Hamilton *et al*. 2005, Cadotte *et al*. 2006b, Pyšek and Richardson 2007, Ordonez *et al*. 2010, van Kleunen *et al*. 2010). In this thesis, I have developed and presented a strict and robust set of species selection criteria to advance our understanding of invasiveness. I have performed empirical work using these criteria to further show that the search for traits that predict plant species invasiveness is a fruitful, informative and valuable exercise.

8.2 WERE THE AIMS OF THIS THESIS MET?

My thesis research focused on the observation that only a small subset of naturalised exotic plant species in Australia have transitioned to become invasive. The determinants of the transition from the stage of naturalisation to invasion (Richardson *et al*. 2000) are poorly understood, yet crucial for our understanding of the mechanisms promoting species invasiveness (Pyšek *et al*. 2008b, Murray and Phillips 2010, Phillips *et al*. 2010a). This research thesis addressed the roles that a range of plant life-history traits contribute to exotic species invasiveness by employing a continental-scale, target-area comparison (with evolutionary considerations). The research presented in this thesis examined patterns of plant trait similarities and differences between invasive and non-invasive species across multiple plant life-history stages, from seeds in the seed bank to germination characteristics to seedling emergence, growth and the traits of mature plants. This thesis has identified several attributes that are linked to the continental-scale invasion success of exotic species across Australia. Therefore, the broad aim of this thesis was fulfilled.

In order to tease out some of the finer details regarding the comparative invasion success of exotic plant species, four specific aims were addressed in this thesis:

1. To determine relationships between introduction-history traits and species invasiveness among exotic plants introduced to Australia by humans since the beginnings of permanent European settlement.

In Chapter 2 of this thesis, I explored several traits linked to plant introduction history for 468 naturalised exotic plant species within Australia, representing 127 distinct taxonomic families. I found that residence time was a significant predictor of invasion success, as was growth form, with vines more likely to be invasive within Australia. Continental origin was found to be correlated with invasiveness, with invasive species more likely to originate from North and South America and less likely to originate from Europe or Australasia. Therefore, this specific research aim has been met. Key plant differences like growth form should be considered when investigating life-history traits in relation to invasiveness in species pools, given that invasive grasses will certainly exhibit a different canopy height, for instance, than non-invasive trees and a comparison between the two may not uncover the correlative evidence needed to better understand species invasiveness. Likewise, a species' minimum residence time within the introduced region should be acknowledged, when possible, as a non-invasive shrub which has been in Australia for less than 10 years is much less likely to have reached its invasive spread potential if compared with a non-invasive shrub which has been naturalised within Australia since the early 1800s.

2. To create a framework for species selection in mensurative and manipulative experiments designed to distinguish life-history traits underpinning invasiveness.
Using introduction-history traits identified as correlates of invasiveness in Chapter 2, I constructed a species selection framework, outlined in Chapter 3, in order to closely examine life-history differences between invasive and non-invasive naturalised plant species while minimising potentially confounding factors. The species selection framework controlled for residence time, growth form, co-occurrence and geographic range size (area of occupancy). Critical to the framework was the incorporation of phylogenetic relationships between invasive and non-invasive species. The dataset of congeneric invasive and non-invasive species established in this chapter was the foundation of all my database and experimental studies in this thesis. Therefore, this specific research aim was also met.

3. To quantify relationships between life-history traits and species invasiveness.
By creating a rigorous species selection framework, I was able to perform life-history comparisons between invasive and non-invasive exotic plant species within the continental-scale, target-area context, thus meeting this third research aim.
Using the framework from Chapter 3, I first conducted an empirical study analysing life-history trait relationships with species invasiveness using a complementary cross-species (CS) and phylogenetically-independent contrasts (PIC) approach. This study was successful in that it detected two life-history traits linked to invasiveness within the naturalised flora of Australia: an increased number of plant dispersal mechanisms and the use of water as a dispersal mechanism. By showing that these two life-history traits were significantly linked to invasiveness and that the traits have diverged with invasiveness in multiple independent phylogenetic radiations, it can be concluded that these life-history traits are important correlates of species invasiveness within the exotic flora of Australia. Studies such as this one underscore the importance of ensuring

the most appropriate and contextually-meaningful selection protocols are in place when performing species comparisons between groups of interest.

Using exotic species that fit the selection criteria, I experimentally compared seed germination characteristics between seven congeneric pairs of invasive and non-invasive species (Chapter 5). I found that the seeds of invasive species germinated more rapidly, but were also more likely to exhibit a 'bet-hedging' strategy by staggering seed germination over a longer period of time, as well as retaining a higher proportion of dormant but viable seeds after a germination-triggering event occurred.

In Chapter 6, I compared seedling traits between invasive and non-invasive plant species using four congeneric pairs to determine whether there were any consistent trait correlations with species invasiveness. The study explored five seedling traits including time to seedling emergence from the soil, seedling height, leaf production, specific leaf area and biomass. I found evidence that some invasive species differ from non-invasives during the seedling stage (e.g. invasive *Coreopsis lanceolata* emerges from the soil earlier, invasive shrub *Salvia coccinea* had higher specific leaf area), but I found no consistent seedling trait explicitly linked to species invasiveness.

4. To understand the role that biotic and abiotic ecological attributes, including the biotic soil community and increased nutrient load play in determining the invasion success of exotic plant species.

This final research aim was met. In Chapter 4, I found evidence on a local-scale that the survival of seeds of invasive species in the soil seed bank was significantly higher than seed survival in non-invasive species. I also found that the application of a fungicide treatment led to a larger increase in seed survival in the non-invasive compared with the invasive species. Thus, I suggested that poorer seed survival in the non-invasive species could be attributed to seed-deteriorating soil-borne pathogenic fungi present in the new range.

An important feature of my experimental work was the consideration of plant phylogeny, not only in the species selection process, but also at the analytical stage. The inclusion of a factor 'genus' in the models meant that the influence of phylogeny on cross-species patterns was explicitly considered. In some cases (e.g. Chapter 4) this was important, as statistical interactions between genus and invasion status emerged, indicating that trait correlations with invasiveness were not always consistent in independent evolutionary tests (i.e. the separate congeneric pairs).

In addition to my main thesis aims, Chapter 7 presented the results of a deeper exploration of the temporal patterns of introduction of 759 exotic plant species to Australia, species native to Central Europe. The main outcome of this work was the identification of three distinct peaks in plant species introductions, with each introduction peak correlating with significant periods of human movement, including the Gold Rush of the 1850's, pre-war 1920's and the digital revolution that was the development of the internet.

8.3 THE ONGOING SEARCH FOR PLANT SPECIES TRAITS DRIVING INVASIVENESS

The comparative approach used in this thesis employed a novel set of species selection criteria with which to compare invasive and non-invasive species. Importantly, not only was a published categorical scheme of invasiveness (Randall 2007) used to start the species selection process, I carefully collected information on residence time, co-occurrence and geographic range size among other attributes to ensure that invasive species were compared with true non-invasive species. In other words, the non-invasive species examined in this thesis weren't just 'waiting in the wings' to overcome a lag period for instance. Nevertheless, a good way forward from the work presented in this thesis will be to use more information about the invasiveness continuum. For example, Davidson and Nicotra (2012) suggest an approach to compare species invasiveness on a sliding scale, comparing 'less invasive' and 'more invasive' species using ecological information and geographic distribution data. By combining approaches to determine the drivers of species invasiveness, a complementary set of answers to the 'what drives invasive species' question will emerge. Therefore, progress towards a general understanding of plant invasiveness can be achieved by pooling all evidence from each research approach together and considering the contexts and merits of each study, from local-scale studies to global, as parts of a bigger picture.

The species traits in this thesis represent mean (e.g. seed mass) and maximum (e.g. plant height as explored in Chapter 3) species values. An alternative approach to this will be to explore the role of phenotypic plasticity for invasiveness, investigating the mean trait values in conjunction with the variances in the trait values a species genotype expresses when exposed to a diverse range of environmental conditions. Plastic responses in plants result from both biotic and abiotic stimuli and can be expressed as morphological, anatomical and physiological shifts in traits. Differences in species plasticity may reflect differences in the ability of plants to naturalise and therefore become invasive in a given environment (e.g. Schlichting and Levin 1986, Poorter and Nagel 2000, Stenstrom *et al*. 2002, Griffith and Sultan 2005). For instance, a species with greater phenotypic plasticity will potentially be more likely to adapt to a broader range of novel environmental conditions, occupy a greater number of environmental niches and therefore become invasive compared to species with low phenotypic plasticity (Bradshaw 1965, Van Valen 1965, Whitlock 1996, Donohue *et al*. 2001, Sultan 2001, Richards *et al*. 2005). Given that the primary goal of invasion ecology research is to enhance our understanding of how some species are able to become invasive in new ranges, including species plasticity in to comparative studies of invasive and non-invasive species may be an important research direction in the future, given the continually changing and shifting nature of the environmental conditions species encounter in the new range.

8.4 EXOTIC SPECIES INVASIONS: THE OUTLOOK FOR AUSTRALIA

Australia is a relatively newly-colonised continent by Europeans (i.e. < 250 years since permanent European settlement), which has provided a unique opportunity to observe patterns of introduction and invasiveness among exotic flora during relatively ‘early’ stages of exotic plant species invasion. Australia also stands out as a continent with fragile ecosystems, continually threatened by processes of change, including human interference, climate change and species invasions. Given Australia’s geographic isolation from all other continents, the introduction of exotic species has been largely a human-driven process and many of our worst invaders have been brought in intentionally by humans for human benefit (as discussed in Chapter 2 and Chapter 7). One example of this is wild Blackberry (*Rubus fruticosus* agg.), a species aggregate that was intentionally introduced by settlers in 1851 as an easy-growing source of food. Blackberry is now considered a Weed of National Significance and covers more than 8.8 million hectares of land in Australia or 1 m in every 100 m of the land surface of Australia. In 2006, it was estimated that annual primary production losses and Blackberry control costs exceeded $70 million AUD (CRC Report 2006). A single species aggregate has spread across Australia on such a vast scale, created so much damage ecologically, agriculturally and economically, and there are many more exotic species which could potentially make the transition to become invasive. Therefore, a priority for Australia's ongoing weed management should therefore be the further enhancement of prediction-based systems which detect as well as prevent the entry of invasive species.

Several decades have passed since the inception of invasion ecology as a research discipline. Predictive life-history traits play a key role in invasive species management, with several invasive species screening programs built around introduction and life-history attributes of plant species. The relative success of these screening procedures provides support that the search for suites of traits that can predict species invasiveness is not a futile exercise (Daehler and Carino 2000, Keller *et al*. 2007, Gordon *et al*. 2008a). Currently Australia uses a three step approach in weed prevention and management: the predictive Weed Risk Assessment (WRA) system, Quarantine import restrictions (AQIS ICON) and the inspection of imported goods (e.g. mailed parcels, shipping ballast) for plant contamination as well as intentional imports.

The WRA system was created in 1997 following an extensive review of Australia's quarantine policies and programs (Nairn *et al*. 1996). The review aimed to help protect Australia’s favourable preventative pest and disease status while ensuring Australia complied with international trade obligations. As a consequence, the WRA system was created as a method of pre-screening exotic plant species using predictive traits so that species with a low likelihood of becoming invasive within Australia can be imported while preventing the importation of other species with a high likelihood of becoming invasive species in Australia. The goal of the WRA is to limit the entry and distribution of potentially-invasive species to Australia and is based on a scoring system of life-history and introduction-history traits known to promote species invasiveness. If a species scores too many points (e.g. too many introduction-history and life-history correlates with species invasiveness), it is not permitted for entry or sale in Australia and the species is registered on the AQIS ICON system with this decision.

In 2007, Keller *et al*. demonstrated that the WRA system produced considerable net bio-economic benefits to Australia within a decade of its implementation. Further to this, Gordon *et al*. (2008a) researched various applications of the WRA system and found that the system rejects an average of 90% of known invasive species and accepts an average of 70% known non-invasive species. Several Australian states and territories have used the WRA system as the basis for determining the weed potential of plants proposed for importation into their respective jurisdictions. The WRA system has also been adopted by New Zealand and modified versions of the system have been tested for use in Bonin, Japan (Kato *et al*. 2006) Hawaii (Daehler and Carino 2000), Florida (Gordon *et al*. 2008b), the Czech Republic (Krivánek and Pyšek 2006) and the Pacific Islands (Daehler *et al*. 2004).

Preventative, trait-based management of exotic species for Australia is a cost-effective method of minimizing the likelihood of future species invasions while also facilitating the importation and trade of important non-invasive species. While on the one hand, the findings of my thesis provide important ecological information furthering our understanding of patterns and processes of biological invasions, on the other hand, my findings can only serve to enhance predictive trait-based programs like the WRA system. Clearly, however, there is a need for serious government investment of resources to make use of all available ecological information to allow close to 100% prediction success of likely invasive plant species in Australia. But even before this, there needs to be recognition and action to prevent the ease with which invasive plant species can enter Australia. During my research, I was surprised by the ease in which I was able to purchase seeds of invasive species within Australia. I performed my own survey of the AQIS ICON system to determine its utility in preventing the introduction and distribution of already-invasive exotic species. Of the 134 ecologically-devastating invasive species identified by Randall (2007) and examined in this thesis, less than two thirds of these species are have a record on the AQIS ICON system as of July 2012 (Figure 8.1), meaning there is no rule in place which restricts (or permits) the entry of these invasive species to Australia. Perhaps even more alarming, of the 82 invasive exotic plant species which do have records on the AQIS ICON system, the seeds of more than half of those species are legal to import to Australia (Fig. 8.2a), as well as live seedlings of 40 known invasive species (Fig. 8.2b).

Identifying already-invasive exotic species yet still permitting their entry and commercial distribution in Australia is a counterproductive contrast to the goals of invasive species management in Australia. I suggest that implementing current scientific knowledge of species invasions in Australia into government policy should be an immediate imperative for weed managers and would certainly be a progressive step on the path to reducing the risk of new outbreaks of known invasive exotic species.

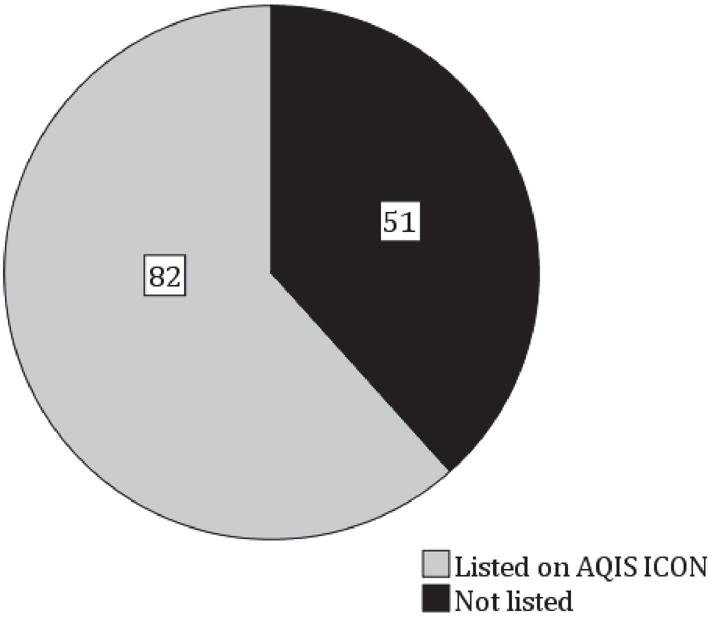


Figure 8.1. Available information on the legal status to import to Australia each of the 133 invasive exotic species listed in Randall (2007) (Source: AQIS ICON database; accessed July 2012).

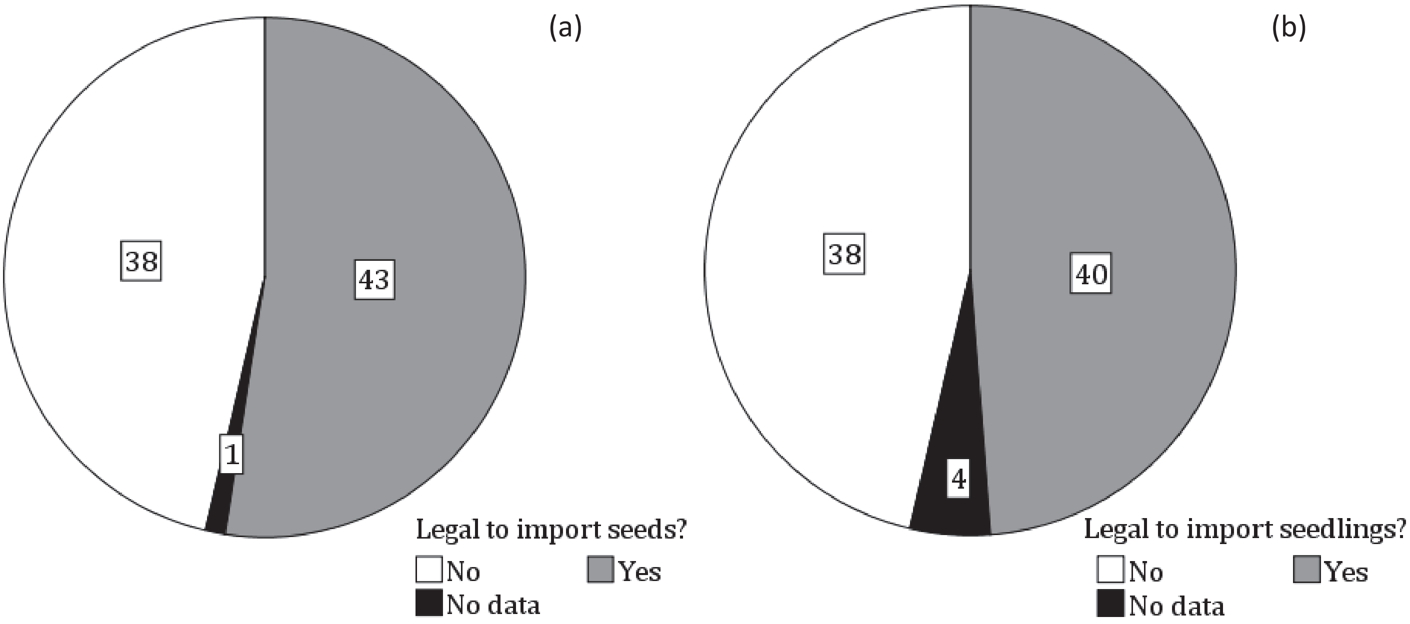


Figure 8.2. Legal status to import (a) seeds and (b) live seedlings to Australia for each the 82 invasive exotic species listed in AQIS ICON (Source: AQIS ICON database; accessed July 2012).

8.5 CONCLUSION

The work presented in this thesis contributes to the quest to identify plant traits facilitating the naturalisation to invasion transition. This thesis used a comparative approach to successfully link exotic plant species invasiveness within the introduced range to plant introduction-history and life-history traits across a range of plant life stages. The approach and findings of this thesis were both built on an important historical body of work examining plant species invasiveness. Given the relative paucity of work focusing on the shift from naturalisation to invasion, arguably the most important process in the invasion pathway, I believe that this thesis has made a meaningful contribution to the field of invasion ecology and has provided information crucial for our understanding and management of the global problem of biological invasions.

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