A comparative study of the reproductive biology and invasive ranges of gorse (*Ulex europaeus*) in the Mount Lofty Ranges of South Australia and central highlands of Sri Lanka

Champika S. Kariyawasam

B.Sc(Hons), M.Sc

School of Biological Sciences

Faculty of Science and Engineering

Flinders University of South Australia

Bedford Park SA 5042

Australia

Fax 82013015

E-mail: kari0020@flinders.edu.au

August, 2013

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Thesis abstract

Ulex europaeus L. (gorse) is a cosmopolitan invasive shrub species native to Europe. This species is classified as a 'Weed of National Significance' in Australia and is also recognized as an invasive species in Sri Lanka. A comparative study was conducted of *U. europaeus* populations located in the Mount Lofty Ranges of South Australia and central mountains of Sri Lanka. The fruit set and fruit to flower ratio, seed production per pod, seed predation and the density of gorse seeds in the upper 5 cm layer of the soil were investigated in gorse populations from late winter to spring in the Mount Lofty Ranges, South Australia and from late November to late January (late wet and early dry season) in the central mountains in Sri Lanka. The results of this study suggest that there are differences in the traits investigated in *U. europaeus* in their invasive range in these two countries.

The threat posed by invasive alien species to native biodiversity is well recognized. Species distribution models (SDMs) are considered one of the most powerful tools to evaluate invasion risk. Forecasting the potential areas of occupancy of invasive species facilitates environmental planners taking early action, before invasive species are introduced or expand their ranges. A species' distribution pattern may also dramatically change under different climate scenarios due to the fact that the rate of invasion by weedy species is often affected by the degree of similarity in the climate of source and reception areas. This study was conducted using the Maxent species distribution modelling software package and utilised presence-only location data to predict the potential distribution of *U. europaeus* in South Australia under current climate conditions. Model predictions using GLM, Bioclim, Domain and Maxent models for the same set of data were compared and Maxent was found to produce a more conservative model. Models fit in South Australia were also used to predict the climate suitability for *U. europaeus* of a climatically distinct area (Sri Lanka) and Maxent was identified as a robust modelling technique to make such projections. This study highlights the importance of applying a distribution model of an invasive species derived in one area to another geographic area.

Declaration

‘I certify that this thesis does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.’

Champika S. Kariyawasam

Acknowledgements

I would like to convey my sincere thanks to people who helped me in numerous ways during my project period in the School of Biological Sciences, Flinders University, South Australia. First and foremost, I would like to thank my supervisors Assoc/Prof. Duncan Mackay and Dr Molly Whalen, School of Biological Science, Flinders University, South Australia for supervising me during the course of my candidature. I am thankful to Duncan who was a patient teacher and gave me kind support at any time, even in his busy schedule. His valuable guidance and scientific advice helped me to complete this thesis. I appreciate Molly's encouragement, suggestions and constructive criticism to improve my thesis.

I would like to thank the Department of Environment and Natural Resources, Government of South Australia and Department of Wildlife conservation, Sri Lanka for permitting me to undertake scientific research within the State's system of conservation reserves. I would like to acknowledge the State Herbarium of South Australia for providing *Ulex europaeus* herbarium records for the study. I acknowledge Dr. James Leary, University of Hawaii at Manoa for providing geo-referenced gorse data of Hawaii for the development of the world distribution map of gorse.

I would like to express my sincere gratitude to my colleague Mr John Marshall, PhD candidate of Flinders University for not only assisting me to become familiar with GIS data-handling but also for his rich discussions. I wish to thank Kieren Beaumont, for his editing skills and for helping me to structure the thesis. I also wish to thank all

my colleagues in the lab and staff members of School of Biology, Flinders University who supported me in many ways.

My special thanks are owed to Maria and Lorinda of the Lutheran Church, Pasadena for their helps and encouragement during my assignment.

I will always be deeply indebted to my family who assisted me in numerous ways to accomplish this project. I will always be deeply indebted to them.

Overview of thesis content

Chapter 1 provides an introduction to the content of the thesis. This chapter contains an overview of the subject and a list of references.

Chapters 2 and 3 of the thesis are based on original findings of the research project done at School of Biological Sciences, Flinders University, South Australia during 2011-2013. These two chapters are written in the format of scientific journal articles. Each of these two chapters contains an abstract, methodology, results, discussion, conclusion, acknowledgement and a list of references and none of these chapters are published yet.

All chapters were written by me with the supervision of my supervisors, Assoc/Prof Duncan Mackay and Dr. Molly Whalen of the Flinders University.

Chapter 1

INTRODUCTION

Plant invasion

The impact caused by invasive species on native biodiversity is widely recognized in addition to the economic impacts (Sakai *et al.* 2001) and public health disasters (Mooney and Hobbs 2000). Invasive species make negative impact on overall structure, function and community dynamics of ecosystems devastating native and indigenous biodiversity (Catford *et al.* 2009). Invasion ecology comprises many hypotheses that discuss the invasion success of species at various spatial and temporal scales (Richardson and Pysˇek 2006; Catford *et al.* 2009). Several factors may influence the success of invasion. Three factors, propagule pressure, biotic characteristics and abiotic characteristics are likely to contribute to the success of an invasion (Catford *et al.* 2009). Recognizing the factors that limit the reproductive success of an invasive species is important for designing plant conservation programs as well as control and management programs, as the adverse consequences of species invasions are complex, interconnected and often entail enormous ecological damage (Mack *et al.* 2000). Among the important potential reasons why invasive plants succeed are lack of predators, availability of favourable niches, habitat alteration and disruption of natives (Mack *et al.* 2000). In addition, several traits of plant invaders, including a persistent seed bank, high dispersal capacity of propagules (Bossard 1991), rapid growth rate or high fecundity (Bellingham *et al.* 2004) can facilitate their widespread colonization of new areas. Successful invaders possess some traits that are not available in unsuccessful invaders (Sakai *et al.* 2001; Pyšek and Richardson 2007). Sakai *et al*. (2001) found that life history traits make species more invasive. However, Williamson and Fitter (1996) concluded that invasion success of a species is related to the abundance and distribution of that species in its native range rather than life history traits.

Several processes driven by human interventions will most likely increase the number of invasive species (Mooney and Hobbs 2000). Human mediated dispersal assist more rapid increases in the range size rather than the natural dispersal (Wilson *et al.* 2009). The majority of plant invaders were purposely introduced into their invasive range (Mack *et al.* 2000) for various commercial purposes. Woody shrubs belonging to the family Fabaceae are recognized as some of the most important weeds in the world (Paynter *et al.* 2003) due to their ecological and economic impacts. Lazarides (1997) report that 296, or *ca.*11%, of the 2733 weed taxa in Australia, are legumes. Thus, studying invasive species belonging to the family Fabaceae has special importance to Australia. The nitrogen requirement of aliens is very much higher than local flora (Pysek *et al.* 1995). Invasive plants increase the level of soil nitrogen possibly due to the mutualisms with nitrogen fixing bacteria which is considered as an important mechanism of non- native plant invaders (Reinhart and Callaway 2006). Plant competition has been tested along a productivity gradient and nitrogen availability exerted strong influences on the success of invisibility (Wilson and Gerry 1991). Plants belong to family Fabaceae are able to engage in root nodule symbiosis with nitrogen-fixing soil bacteria, called rhizobia (Wang *et al.* 2012) and the nitrogen fixation associated with legumes were at least 10 times higher than the non legumes (Skeffington and Bradshaw 1980).

Reproductive biology of invasive plants

Understanding the invasiveness of a particular plant species in different, novel environments is vital for effective management (Sheppard *et al.* 2002). The invasion success of a plant species often depends strongly on the nature of its reproductive biology. Flowering and fruiting phenologies of a plant are very important in reproductive biology (Elzinga *et al.* 2007; Atlan *et al.* 2010). Research studies conducted for invasive plants show that there is a considerable variation in flowering and fruiting phenology throughout their native and invasive ranges, not only among sites but also among individual bushes within sites (Tarayre *et al.* 2007; Bowman *et al.* 2008). Successful invasions by certain invasive plants are facilitated by their ability to change flowering time according to climatic conditions of the habitat (Bowman *et al.* 2008). Several environmental factors can affect the phenology of a particular plant species (Rathcke and Lacey 1985; Ims 1990; Pico and Retana 2001). Changes in flowering time and duration of invasive plants may lead to a scarcity of pollinators for reproduction (Bowman *et al.* 2008), and this is an important area to be researched in a wide range of infested habitats. Invasive species show unusual flowering and fruiting phenology (Bowman *et al.* 2008). According to a previous study, the flowering and fruiting phenologies of gorse (*Ulex europaeus*) has a genetic basis (Atlan *et al.* 2010).

Species distribution modelling of invasive plants

Native biodiversity is diminishing at an alarming rate and invasive alien species are considered to be an important driver of biodiversity loss (Neubert and Parker 2004). The threat posed by biological invasion is complex, possibly irreversible and brings long-term impacts (Holmes 2010). Understanding the current and potential geographic distribution patterns of invasive species is fundamental for decision makers for managing invasive alien species (Kearney *et al.* 2008). Predictive geographical modelling is increasingly used as a tool to assess the risk posed by invasive species and to predict the range shift of invasive species (Guisan and Zimmermann 2000). However, the ability to predict the potential geographic distribution of range shifting species is challenging (Kearney *et al.* 2008) because they often violate equilibrium assumptions and make challenges to distribution modelling (Elith *et al.* 2010). Invasive plants take advantage of changing climates and respond to shifting niches more easily than native species which are slower to respond under changing climates (Dukes and Mooney 1999). Today, species distribution modelling has been recognized as one of the key tools of species invasion risk assessment although only a handful of studies have attempted to predict the range shift of invasive plants under climate change scenarios (Crossman *et al.* 2011).

History of invasion of gorse in Australia and Sri Lanka

Gorse is an early introduction to Australia (Parsons and Cuthbertson 1992; Richardson and Hill 1998). It was recorded in New South Wales as early as 1803 and listed in a Tasmanian nursery catalogue in 1845 (Parsons and Cuthbertson 1992). It was brought to Australia for ornamental purposes and also as a hedge plant, escaped and reported as naturalised in Australia as early as 1889 (Parsons and Cuthbertson 1992; Richardson and Hill 1998). Today, gorse is a noxious plant in Australia and listed as one of the 20 Weeds of National Significance (Thorp and Lynch 2000) with most infestations occurring in Victoria and Tasmania (Ireson *et al.* 2008). Gorse infestations also occur in several other states in Australia, such as South Australia, Australian Capital Territory and New South Wales, at various levels of extent and magnitude. In Australia, gorse is common on creek banks, road sides, neglected areas, forest margins, hedges and mine dumps (Thorp and Lynch 2000).

Gorse occupies over 23 million hectares in Australia leaving 1 million hectares of land unproductive. However, the potential distribution based on climate modelling is predicted as 87 million hectares (Gouldthorpe 2006). The annual cost of gorse management to agriculture and forest industries in Australia has been estimated as $7 million in 2000 (Gouldthorpe 2006). According to the above authors, gorse has one of the highest economic costs of management compared with other noxious agricultural and forestry weeds in Australia.

Gorse was introduced to Sri Lanka as early as 1888 (during the colonial period) by the British through the Botanic Gardens, Peradeniya (Wijesundera 1999). They planted gorse in their gardens in Nuwara Eliya from where they probably escaped. Today, gorse is confined to a few small populations in the Horton Plains National Park and Nuwara Eliya in the central highlands of the country, but there are no records of how it migrated to Horton Plains. Gorse is considered as an invasive plant in Sri Lanka too. According to a study (Devendra *et al.* 1998), gorse infests approximately 6 hectares in Horton Plains.

Research problem

Gorse is considered a notorious invader that threatens native plant species diversity. The ecological and economic damage caused by gorse is significant (Ireson and Davies 2012), and there is an urgent need to control and manage the species. Thus, it is important to study and understand the factors contributing to the widespread distribution of gorse.

Studying the reproductive biology of the species is also important to understand the factors contributing to widespread colonization. Developing species distribution models is important for several scientific applications in conservation planning and management of a species. Since gorse is strongly influenced by climatic parameters (Hill and Gourlay 1991; Hill *et al.* 2007; Tarayre *et al.* 2007), the potential area of occupancy of this species may be predicted by suitable distribution modelling techniques. This will help in identifying the habitat requirements of gorse and provide a better understanding of the potential threat posed by this species on natural resources in the study areas.

Aims and objectives

Reproductive biology

Assessments of the phenology and soil seed bank of gorse are needed to understand the factors influencing their high reproductive efficiency and invasiveness. Given that self-pollination is not common in this species (Yeo 1993), their high reproductive success could be due to an abundance of pollinators for outcrossing. In this comparative study of Australian and Sri Lankan gorse populations, we aimed to investigate some aspects of the phenology and seed bank dynamics of gorse that affect their invasiveness in the two study areas and to investigate the following aspects in the invasive range in these two countries,

a) the levels of fruit set, seed production per pod and seed predation in these populations during the study period, and

b) the level of seed bank density that contributes to successful invasion of gorse.

Species distribution modelling

The potential distribution of gorse in South Australia and possible range expansion in Sri Lanka were predicted using Maxent software and other multiple species distribution modelling techniques. The resulting model predictions should provide valuable information for land managers to make relevant conservation actions.

The following modelling scenarios were examined;

a) Species distribution modelling using Maxent software in South Australia to identify potential areas of *Ulex europaeus* distribution,
b) Model projection to Sri Lanka using Maxent software to identify possible range expansion of *U. europaeus*,
c) Multiple SDM model comparisons for *U. europaeus* in South Australia,
d) Model projection to Sri Lanka using multiple SDM models for *U. europaeus.*

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Chapter 2

Comparative study of the reproductive biology of gorse (*Ulex europaeus*) in the Mount Lofty Ranges of South Australia and central highlands of Sri Lanka

Champika S. Kariyawasam, Duncan A. Mackay and Molly A. Whalen

B.Sc(Hons), M.Sc

Flinders University, School of Biological Sciences, GPO Box 2100, Adelaide, SA 5001, Australia

Kariyawasam, *et al*. (unpublished)

Key words: fruit : flower ratio, predation, seed bank density, seed production, *Ulex europaeus*,

ABSTRACT

The present study aims at understanding how certain traits of gorse (*Ulex europaeus* L.) contribute to its reproductive success in two climatically distinct regions in its invasive range, South Australia and Sri Lanka. We examined several traits, namely fruit set (fruit:flower ratio), seed production per pod (number of seeds per pod), pod predation and the density of seeds in the upper 5 cm layer of the soil seed bank. Field work was conducted from late winter to spring in the Mount Lofty Ranges, South Australia and late November to late January (wet and dry season) in the central mountains in Sri Lanka. Our results suggest that the reproductive success of gorse in Sri Lanka, in terms of fruit:flower ratio, is less than that of gorse plants in South Australia. However, this difference may be due to non-equivalent time between assessments of flower and fruit numbers. Results also suggest that gorse populations in Sri Lanka had higher seed numbers per pod compared with gorse populations in South Australia. We found that predation of pods was negligible in our study sites in both countries during the period of study, although the literature show that predation in gorse strongly depends on the time period. We observed significant differences in the density of gorse seeds in the top 5 cm layer of the seed bank between 3 m away from shrubs and under gorse shrubs. This estimated density of gorse seeds under shrubs in Sri Lanka was 2141 / m^2 which was 1.5 times higher than that of South Australia.

INTRODUCTION

Several factors may influence the invasiveness of a particular plant species. Recognizing the factors that limit the reproductive success of an invasive species is important for plant conservation and management. Understanding the effects of different environments in limiting invasiveness is also important for effective management of widely spread invasive species (Sheppard *et al.* 2002). Several traits of plant invaders, such as having a persistent seed bank, high dispersal capacity of propagules (Bossard 1991), nitrogen fixation ability (Skeffington and Bradshaw 1980 ; Wilson and Gerry 1991) and rapid growth rate or high fecundity (Bellingham *et al.* 2004) support widespread colonization by invasive plants in a given habitat.

Ulex europaeus L. (Fabaceae), popularly known as gorse, is a native of Europe (Parsons and Cuthbertson 1992; Markin and Yoshioka 1996; Ireson *et al.* 2008; Atlan *et al.* 2010; Ireson and Davies 2012) and the British Isles (Hill *et al.* 2001). Gorse is a non-destructive and commercially important plant in its native range but it behaves as a notorious invader in most of its exotic range (Atlan *et al.* 2010). It is a common weed in more than 15 countries in the world (Markin and Yoshioka 1996) from temperate to tropical areas and from coastal areas to mountains along a wide latitudinal and altitudinal gradient (Fig.1). Gorse distribution is limited by temperature and widely distributed in areas where the monthly minimum temperature is higher than 2°C (Centre for Environmental Management University of Ballarat 1999). The recognition of gorse as a globally important weed is illustrated by the listing of this species in the top 100 of the world's worst invaders prepared by the World Conservation Union based on two criteria; the serious impact on biological diversity / human activities and serious issues of biological invasion (Lowe *et al.* 2000). Gorse is listed as a Weed of National Significance in Australia (Gouldthorpe 2006) and is an interesting study species for invasion biologists due to its successful invasion of a wide range of geographic and climatic areas.

Though gorse has been identified as an aggressive invader in its exotic range (Hill *et al.* 2007; Atlan *et al.* 2010), literature on gorse regarding its environmental impacts is limited. Gorse plants shade out seedlings and compete with young trees and reduce the productivity of pastures and plantation forests in New Zealand (Hill *et al.* 2000; Barton *et al.* 2003). Gorse reduces the recreation value of the land and burns easily creating fire hazards (Centre for Environmental Management University of Ballarat 1999).

Denyer *et.al* (2010) report that gorse reduces the species richness of the vegetation in the absence of grazing; however, gorse increases the soil nutrients making heterogeneity in productivity across the sites. According to one estimate, gorse occupies over 23 million hectares in Australia leaving 1 million hectares of land unproductive. However, the potential distribution based on climate modeling is predicted as 87 million ha (Gouldthorpe 2006). Thorp and Lynch (2000) analysed the economic costs attributed to 35 agricultural and forestry weeds in Australia and listed three species including gorse under the highest cost category which is over $ 5,000,000.

Gorse is a spiny, multi-branched, medium to tall perennial shrub (Markin and Yoshioka 1996; Richardson and Hill 1998; Bowman *et al.* 2008; Atlan *et al.* 2010). Plant height varies from 1-4 m (Atlan *et al.* 2010) and the dark green spiny leaves are 1-3 cm long and usually alternate (Parsons and Cuthbertson 1992). Gorse plants live up to 30 years (Lee *et al.* 1986; Gouldthorpe 2006) and attain reproductive maturity normally at four years of age (Atlan *et al.* 2010). Reproduction of gorse occurs by seeds only and seed production of gorse is abundant (Moss 1959; Centre for Environmental Management University of Ballarat 1999).

Gorse is an opportunistic legume species (Leary *et al.* 2006) very successful in disturbed habitats. It has the ability to thrive in nutrient poor soil (Lee *et al.* 1986; Clements *et al.* 2001; Leary *et al.* 2006) this could be due to its nitrogen fixing ability. It is a generally accepted fact that most of the weeds are nitrogen fixing legumes (Richardson *et al.* 2000) and this is common for gorses too (Leary *et al.* 2006). Being nitrogen fixing legume gorse is benefited over other plants to invade nitrogen poor habitats (Leary *et al.* 2006). Therefore this can be considered as an important character of invasion success of gorse.

The flowering and fruiting phenologies of a plant are very important aspects of its reproductive biology (Elzinga *et al.* 2007; Atlan *et al.* 2010). Research studies conducted on gorse show that there is considerable variation in flowering and fruiting phenology throughout its native and invasive ranges (Markin and Yoshioka 1996; Tarayre *et al.* 2007; Bowman *et al.* 2008; Atlan *et al.* 2010).

Gorse flowers are bright yellow, pea-like, and approximately 2 cm long (Parsons and Cuthbertson 1992; Markin and Yoshioka 1996; Richardson and Hill 1998). Flowering may be very much synchronized on different branches of an individual plant but can vary significantly among plants in the same population (Markin and Yoshioka 1996). Flowers are hermaphroditic (Atlan *et al.* 2010) and rich in pollen but nectarless (Tarayre *et al.* 2007). Each flower typically bears 10 stamens and 12 ovules (Bowman *et al.* 2008; Atlan *et al.* 2010). In its native range, gorse flowers mainly in spring (Bowman *et al.* 2008); however, in its invasive range, it shows great variation in flowering phenology (Bowman *et al.* 2008; Atlan *et al.* 2010). In the invasive range, flowering can happen once or several times a year and may last for a shorter or much longer period than in its native range (Moss 1959; Hill *et al.* 1991; Markin and Yoshioka 1996). Flowering intensity in gorse can be high and variable; a single branch can produce 500 to 1000 flowers over a 2-3 month flowering period (Markin and Yoshioka 1996).

The literature on the breeding system of gorse is somewhat complex and confusing because according to the literature it is not clear whether the self pollination of gorse is prevented due to self - incompatibility of gorse flowers or due to the adaptations of flowers to avoid self-pollination. (Markin and Yoshioka 1996) report that gorse flowers are not self-pollinating, and Stokes *et al.* (2006) report that they are self-incompatible and need an insect visit for seed set. Yeo (1993) notes that Fabaceae flowers have adaptations to prevent self-pollination, such as an unavailability of stigmatic fluid when pollen is shed or by physiological self-incompatibility. In self-incompatible plants, pollinators play a key role in plant reproduction by promoting outcrossing (Elzinga *et al.* 2007). Plants may rely fully or partly on one or more animal pollinators for reproduction (Elzinga *et al.* 2007). The primary pollinators of gorse are honey bees (*Apis mellifera* L.) and bumblebees (*Bombus* spp.), and the sole reward for these insects is pollen (Bowman *et al.* 2008). The pollination success of gorse depends not only on the pollen transfer dynamics related to the foraging behavior of pollinators, but also on the frequency of flower visits by them (Suzuki 2003). How the pollination success of gorse plants links with the great variation in flowering phenology is a complex issue that has been studied inadequately.

Gorse seed pods are ovoid to linear-oblong in shape, hairy and reach a maximum length of 1-2 cm (Parsons and Cuthbertson 1992; Richardson and Hill 1998; Tarayre *et al.* 2007). Young gorse pods are green and soft but turn dark brown and harden at maturation (Atlan *et al.* 2010). Pods are enclosed by tan-coloured calyx bracts and dehisce explosively, resulting in the ballistic dispersal of seeds (Tarayre *et al.* 2007). Pods usually contains 4-5 seeds which are 1.5-2 mm in diameter (Markin and Yoshioka 1996). Soft immature gorse seeds are light green in color and turn yellow and then olive green to brownish with maturation. Mature gorse seeds are shiny and harder. A prominent characteristic of gorse seeds is the 'elaiosome', an orange colored fleshy structure located at the base of each seed which attracts ants (Markin and Yoshioka 1996). The elaiosome is considered to be an important food reward for ants that facilitates seed dispersal by them (i.e. myrmecochory) (Edwards *et al.* 2006). The above authors have cited several benefits of myrmecochory to the plant which includes providing better conditions for seedlings to grow and avoiding competition by parent plant and other competitors.

Few studies have investigated flower and pod production of gorse (Tarayre *et al.* 2007; Atlan *et al.* 2010) in its native range and comparative data from its invasive range are also lacking. Since the phenology and growth of gorse in its native and invasive ranges are quite different (Moss 1959), a more comprehensive, quantitative assessment is still needed to estimate levels of flower and pod production by gorse in its invasive range. Such an assessment will provide a better understanding of the role of reproductive biology in the invasive success of gorse plants.

The amount of seed set by gorse plants may vary depending on the level of pollination, availability of resources, abundance of seed predators and pathogens (Pico and Retana 2001). As for most plant species, gorse plants shed the majority of their seeds under the canopy of the parent plant (Hill *et al.* 1996) where there is a low probability of successful germination under the shade of the canopy. But, since gorse has a long-lasting seed bank (Hill *et al.* 2001), seeds could later be dispersed by some other mechanisms (i.e. by biological or physical agent), allowing colonization of new localities later.

Natural enemies of gorse were not available in the invaded range at the time of their introduction and hence pods were not attacked by seed predators; however, seed predators were introduced afterward for the purpose of biological control (Hornoy *et al.* 2011). Gorse pods can be infested by a specific weevil, *Exapion ulicis* (Apionidae), and by larvae of the moth *Cydia succedana* (Tortricidae), at varying levels of infestation (Atlan *et al.* 2010). Research shows that there are differences in gorse seed production and seed predation in various time periods of the year. In the native range, long flowering plants produced more pods in spring than winter and they suffered a high rate of seed predation (Bowman *et al.* 2008). In the invasive range in New Zealand, gorse produces more seeds in summer than winter (Moss 1959). Accordingly, the levels of gorse pod infestation by weevils in summer are generally 20-40 percent but predation is negligible in winter. Several biological control programs have attempted to control gorse using these predators with varying levels of success (Markin and Yoshioka 1996; Ireson and Davies 2012). The gorse seed weevil (*Exapion ulicis*) was released in Australia in 1939 and currently it is well spread through out the range of gorse in Australia (Ireson and Davies 2012). The success of this agent is not satisfactory since it does not affect autumn seed pods. The gorse spider mite (*Tetranychus lintearius*) and gorse thrips (*Sericothrip staphylinus*) which were released in Australia in1998 and 2001 respectively, are well established but the impact is not sufficient (Department of Primary Industries 2008). The gorse soft shoot moth (*Agonopterix umbellana*) has been introduced as a successful biological control agent in several countries and was approved for field release in Australia in 2007. Understanding the phenology of the plant species is critical for the success of most biological control programs, as success depends on the proper synchronization of the biological control agents' life cycles with the appropriate life stage of the target plant (Markin and Yoshioka 1996). However, a comprehensive study is still needed to understand the level of pre-dispersal seed predation necessary to control gorse infestations.

The gorse seed weevil *Exapion ulicis* which was used as the first biological control agent of gorse was introduced to Australia in 1939 (Ireson and Davies 2012). Since then, four other agents *Tetranychus lintearius*, *Sericothrips staphylinus*, *Agonopterix umbellana* and *Cydia succedana*, have been investigated for release in Australia at various levels of success (Hill *et al.* 2008). Use of herbicides for gorse management is economically not feasible (Hill *et al.* 2008). Gorse management could be more benefited by integrated control techniques, however; selection of best suite of control techniques for a specific situation could be most important and challenging (Hill *et al.* 2008). In this context, predictions based on species distribution modeling can play an important role. In South Australia, NRM boards and the National Gorse Task Force actively committed on management and eradication of gorse in the region and achieved a great success (National Gorse Task Force 2011). Though, there is no concerted effort on gorse management in Sri Lanka, our modeling results reveal that climate has probably limited the spread of gorse to the central mountains.

The seed bank often plays a vital role in determining the invasive success of a particular weed (Hill *et al.* 2001). Therefore, studying the seed bank dynamics will not only provide a good understanding of how invasiveness is controlled but will also assist conservationists in minimizing re-invasion and developing policies to exclude noxious plants (Hill *et al.* 1996) from areas of high conservation concern.

Gorse seeds can remain dormant in the soil seed bank for 28 years (Moss 1959) and seed bank dynamics vary from site to site (Hill *et al.* 2001). As Markin and Yoshioka (1996) point out, despite several control attempts, gorse remains well-established in Hawaii mainly due to a huge seed bank in the soil. Under mature bushes, there can be as many as 40,000 gorse seeds per m^2 (Gouldthorpe 2006). There are conflicting findings regarding the different depths in the soil that contain higher amounts of seeds. In New Zealand, Ivens (1978) found an average of 10,000 seeds/m^2, of which 50% were in top 2.5 cm and 75% were in the top 5 cm of soil. He also found that an annual seed fall of 500-600 seeds/m^2. Hill *et al.* (1996) report similar results in their study in New Zealand with a seed fall under gorse bushes of 677 seeds/m^2. The amount of seed fall of gorse in a particular site could also vary depending on the level of pre-dispersal predation (Ivens 1978; Rees and Hill 2001). Gorse seeds are generally deposited under the canopy with a peak at the canopy margin and seed fall gradually declines away from the margin and is very low at 3 m away from the bush (Hill *et al.* 1996). Examination of the seed bank density away from the canopy provides useful information about the regeneration potential of the species in adjacent areas. Gorse seed bank is declined due to germination or death of seeds, however; the losses could be mainly due to germination (Rees and Long 1993; Rees and Hill 2001). A comprehensive long-term study is needed to achieve the ultimate objective of determining the amount of seeds needed in the seed bank to maintain a viable gorse population.

Aims and objectives

In this study, we aim to determine some aspects of phenology and seed bank dynamics of gorse that contribute to invasiveness in the two study areas. Since this is a comparative study, our main focus was not to find absolute values but to relate each trait between the two countries.

METHODOLOGY

Study sites

This study was carried out in three gorse populations located in the Mount Lofty Ranges of South Australia. Study populations were located in the Belair National Park (-

35°0’29.41” S, 138°40’43.9” E) and near the towns of Littlehampton (-35°2’35.73” S, 138°51’48.46” E) and Mount Barker (-35°4’10.93” S, 138°50’33.08” E). The Mount Lofty Ranges have been identified as a centre of plant species richness and endemism (Crisp *et al.* 2001). This area is considered as one of 15 national biodiversity hot spots in Australia (Guerin and Lowe 2013). The Adelaide and Mount Lofty Ranges region is a biogeographically unique area in Australia encompassing a broad range of vegetation types (Department for Environment and Heritage 2009). This region is home to over 1,500 native vascular plant species, over 450 native fauna species including over 75% bird species recorded in South Australia (Department for Environment and Heritage 2009). However, biodiversity of this region is depleting due to the impact of invasive species and land fragmentation (Crossman *et al.* 2011). In this area, gorse has successfully invaded native vegetation and displaced the native understorey vegetation and grasses (Dewar *et al.* 2006). The Mount Lofty Ranges is a relatively hilly area with elevations up to 700m and a Mediterranean climate characterised by hot, dry summers and cool, wet winters (Department for Environment and Heritage 2009; Crossman *et al.* 2011).

In parallel, a similar study was conducted in a geographically distinct small gorse population located in the central mountains in Sri Lanka. Study sites were located near the town of Nuwara Eliya (6°57’49” N, 80°46’7” E), at Kirigalpota nature trail in Horton plains national park (Horton Plains site 6°57’40” N, 80°46’19” E) and closer to Horton Plains park entrance (Horton Plains site 6°47’58” N, 80°48’6” E). The prevailing forest type in this area is wet montane evergreen forests (Ministry of Forestry and Environment 1998). Around 50% of tree species in these forests are endemic to the country (Gunatilleke 2006). This is also home to about half of country’s endemic birds (Pethiyagoda and Gunatilleke 2006). In these areas, though the populations are small, gorse has successfully invaded the upper-montane grasslands, threatening the native plant biodiversity. Annual rainfall in this area ranges from 2500 – 5000 mm however, the temperature is substantially lower (Ministry of Forestry and Environment 1998). Central mountain of Sri Lanka is significantly important hydrologically since it safeguards the catchment areas of all of Sri Lanka’s major rivers. The prevailing soil type in this area is red-yellow podsolic (Ministry of Forestry and Environment 1998). Top soil of the area is acidic and rich in organic matter due to slow rate of decomposition (Ranasinghe *et al.* 2007).

Field work was conducted from late August to late October (late winter to spring) in the Mount Lofty Ranges, South Australia and late November to late January (late wet and early dry season) in the central mountains in Sri Lanka. Three gorse populations were chosen in each geographic study area. In South Australia the distance between populations varied from 5 km to 30 km whereas it was 1 km to 30 km in Sri Lanka.

Fruit set and fruit: flower ratio

Ten plants were randomly selected in each sample site (population), and on each plant, five shoots were randomly selected. Therefore, there were 50 shoots used to examine the level of fruit set from each population. Altogether there were 150 shoots from the Australian populations and 150 shoots from the Sri Lankan populations.

All pods, fading flowers and immature buds were removed from the selected shoots, leaving only open flowers and mature buds. In some cases when the shoots contain numerous flowers, excess flowers were also removed to make counting easier.

The total numbers of flowers in full bloom were counted on the selected shoots and shoots were marked with color tapes and tagged. Plants were allowed to fruit and the tagged shoots were inspected after 4-6 weeks. The numbers of fruits (pods) on each shoot were counted and monitored for fruit production. The fruit to flower ratio was calculated for each shoot.

Seed production per pod

The mean number of seeds in mature gorse pods was investigated. In each visit, 50 pods were harvested in each population randomly. They were dissected and the number of seeds in each pod was calculated. Infested pods or pods with rotten or damaged seeds were not considered for the seed production study. Pods were not collected from plants that have been tagged to test other aspects of the study. The mean number of seeds per pod at each visit was calculated at each study site.

Pod predation

The percentage of infested gorse pods out of all mature pods was investigated. In each visit, 50 ripe pods were harvested in each study site randomly. They were dissected and observed for infestation by predators. Fully or partly damaged pods were considered as infested. The percentage of infested pods at each visit was calculated separately at the population level.

The size of the seed bank

At each study site, one quadrat (15 cm ×15 cm) was placed randomly beneath the crown of each of ten gorse plants and in each quadrat the upper soil layer (top 5 cm) was removed for counting of gorse seeds. Thus, altogether thirty soil samples were taken from three study sites in each geographic area. All samples were bagged and numbered separately for further analysis.

Quadrats were also placed 3 m away from gorse plant crowns so that each quadrat did not have any other gorse plant within a radius of 10 m. Ten soil samples were taken from each study site. Therefore altogether there were thirty soil samples from outside gorse canopies from each geographic area. All samples were bagged and numbered separately for further analysis.

Soil samples were sieved through a 3 mm mesh-sized sieve. The fraction sieved through the mesh was retained and was sieved again through a 1 mm mesh-sized sieve. The fraction retained in the final sieve was used for the examination of seeds. Using this method, we could extract soil samples of between 1-3 mm granules in size in which gorse seeds should be embedded according to their size. Gorse seeds are normally around 2 mm in size (Markin and Yoshioka 1996) and can be easily identified by their heart-shaped, olive green, shiny appearance. In each sample, gorse seeds were taken out and examined under a microscope. Seeds contained in each sample were counted. The measurements were standardized to the square metre.

Germination trials

Germination tests were conducted for gorse seeds that were recovered from 20 soil samples of the upper 5 cm layer of seed bank in Belair National Park. Seeds from each of the 20 soil samples (over 350 seeds in total) were placed in separate petri dishes. Petri dishes were kept in a glass house at Flinders University in autumn 2012 and were watered regularly to maintain moist conditions. The number of new germinants was recorded every fourth day over a period of 2 months. All seeds which did not germinate were scarified using a scalpel after a two-month period, and the germination of these seeds was recorded. Seed viability of the seeds which did not germinate after scarification was determined by dissecting the embryo. The germination test in Sri Lanka was conducted in the Kurunegala area where the average temperature is around 30ºC. We did not conduct a germination test in the central highlands due to inadequate facilities and time.

Analysis

Analyses were done in the R program (R Development Core Team 2012) with the support of the packages ‘lattice’ (Deepayan 2008) and ‘lme4’ (Bates *et al.* 2012). Fruit:flower ratio, number of seeds per pod, percentage pod predation, and log (seed number) in the seed bank were treated as response variables and study sites were taken as the explanatory variable.

Generalized Linear Mixed Models (GLMM) were used for statistical analysis. The magnitude of response variables was quantified across study sites. Analysis was structured to facilitate comparison across countries. The significance of the effects was tested independently for each of the study site. Thus, we treated study sites as random effects within countries which were treated as fixed effects. For binomial seed predation data we used a generalized linear model (family binomial).

RESULTS

Fruit set and fruit: flower ratio

Gorse populations in South Australia show considerable variation in flowering phenology. In some sites (e.g. Littlehampton), gorse was flowering in early spring while in some other sites (e.g. Mount Barker) at that time, gorse bushes were at the stage of onset of fruiting.

Fruit:flower ratios (fruit set) were calculated and plotted for each study site across two countries (Fig. 2). Fruit set data were not collected from Mount Barker because the gorse population at that study site had already finished flowering by the time we did our experiment. Gorse populations in South Australia show average fruit set values of 86.9 and 83.4 in two study sites, namely Littlehampton and Belair respectively compared to the populations in Sri Lanka which show average fruit set values of 58.8 and 11.9 in two sites namely Horton Plans site 1 and Horton Plains site 2 respectively ($z = -2.476$, $P < 0.05$). Table 1 compares findings of the present study with native range data.

Seed production per pod

The average seed number per pod across all sites in South Australia is 2.9 whereas it is 3.7 in Sri Lanka. The mean number of seeds per pod in three sites of Sri Lanka are 3.8, 3.9 and 3.4 (Nuwara Eliya, Horton Plains site 1 and Horton Plains site 2 respectively) whereas they are 3.1, 2.5 and 3.1 (Littlehampton, Belair and Mount Barker respectively) in South Australia. We found a range of 1-8 seeds in pods from gorse populations in South Australia; whereas the range was 1-12 in gorse pods in Sri Lanka.

The number of seeds in a gorse pod was graphed against study areas in the two countries (Fig. 3), and the plot showed a similar median value in most of the study sites. However, we noticed several outliers that are much bigger than the rest of the data.

We compared the number of seeds per pod across study sites in two countries using GLMM. The analysis revealed that there is a highly significant difference ($z = 3.758$, $P < 0.001$) in the mean number of seeds per pod in gorse populations between the two countries, South Australia and Sri Lanka. However, given the similarity of medians shown in Figure 3, this result must be interpreted cautiously as it probably arises from the few high outlier values from the Sri Lankan populations.

However, according to a comparative study of the average number of gorse seeds per pod in two regions in native range (Brittany, France and Scotland , UK) with two regions in invasive range, (Reunion Island and New Zealand), Hornoy *et al.* (2011) concluded that region and range effects were not significant.

Pod Predation

Predation of pods was negligible in our study sites in both countries during the time of our study. Predation was at zero level in all study site in South Australia. However, we observed some predators, presumably *Exapion ulicis,* in South Australia during our field work. We observed slight predation (<4%) in two study sites in Sri Lanka (Horton Plains site 2 and Nuwara Eliya). Data were analysed using a generalized linear model (family binomial) and no significant difference in average levels of pod predation was observed between countries ($z = 0.005$, $P>0.05$).

The size of the seed bank

We compared the density of the gorse seed bank in two locations (under shrubs and 3 m away) between countries. The density of gorse seeds in the top 5 cm layer of the soil showed a marked decline 3 m away from shrubs compared with that under gorse shrubs (Fig. 5). The analysis shows that there is a highly significant difference ($z = 15.470$, $P< 0.001$) in the density of gorse seeds in the seed bank between 3 m away from shrubs and under gorse shrubs.

We compared average seed bank densities across study sites in the two countries using GLMM. The density of gorse seeds in the top 5 cm layer of the seed bank under shrubs across all sites in Sri Lanka was 1.5 times higher than that of South Australia. The estimated average density (mean±standard error) was 2141±732.65 seeds/m^2 in Sri Lanka and 1419±211.95 seeds/m^2 in South Australia. This difference is statistically highly significant ($z = -3.659$, $P < 0.001$).

Germination trials

Around 42% of gorse seeds extracted from the soil seed bank germinated without any treatment over a period of two months.

Out of all non-germinated seeds approximately 84% germinated within one week after scarification. Therefore, out of all gorse seeds, around 91% seeds germinated both by initial germination trial and by scarification of non-germinated seeds. Most of the seeds that did not germinate after scarification were viable and few seeds were removed due to fungal infection. Our seed germination trial in Sri Lanka, in an area with average room temperatures around 30ºC, was not successful. None of the seeds germinated and most were affected with fungal contaminations. The climate in this area is hot year-round and slightly drier than the central mountains where gorse occurs.

DISCUSSION

The present study addressed four aspects of the reproductive biology of gorse: fruit set (fruit:flower ratio), the average number of seeds in a pod, pod predation and seed bank density. Our aim was to understand how certain traits that may contribute to the reproductive success of gorse differ between localities within its invasive range. Therefore, the main intention of this study was a comparative assessment of each trait. However, Table 1 compares results we obtained with results of some studies done in the native range. This table illustrates that the traits considered in this study show trends of higher invasive potential in the invaded range than in the native range.

Fruit set and fruit:flower ratio

The fruit set of an individual plant in a population depends on several factors, such as availability of suitable pollen, pollinator intensity, level of resource allocation for fruit set by the plant, intensity of seed predation and viability of ovules and seeds (Agren and Willson 1992). However, information on relative contribution of these factors on seed or fruit formation of gorse is lacking.

Our results suggests that reproductive success of gorse in Sri Lanka, in terms of fruit:flower ratio, is less than that of gorse plants in South Australia. While conducting the study, all pods, fading flowers and immature flower buds were removed from censused shoots, leaving only open flowers and mature flower buds. This can possibly lead to allocation of more resources to the remaining flowers leading to a higher fruit set if the plants were pollen or resource limited. In contrast, using a perennial woodland herb *Geranium maculatum*, Agren and Willson (1992) showed that seed production is not resources limited. The same study suggested that the amount of pollen received is not a factor limiting seed production in open pollinated plants. The same methodologies were employed in both locations in this comparative study, so that the results should be broadly comparable, however how excess resources or pollen affect pod production in gorse is not certain and it is possible that these effects differ between the study locations.

Scotch broom (*Citissus scoparius*) which is an ecologically similar species to gorse (Zielke *et al.* 1992) has a fruit to flower ratio of approximately 1/4 under open pollination conditions in Australia (Simpson *et al.* 2005), which is quite similar to the results we observed in Sri Lankan gorse (0.25± 0.025)). Based on studies in Australia, USA and Japan, Simpson *et al*. (2005) found that the efficiency of honey bees as pollinators varies extensively among those continents. According to our results the estimate of fruit:flower ratio for gorse in South Australia is considerably higher than the value we obtained for gorse in Sri Lanka. However, fruit production was observed before ripening (browning) of pods on experimental plants in South Australia and it was observed during the ripening stage on experimental plants in Sri Lanka due to the timing of field work. This difference in timing may have caused differences in estimates of fruit set. The additional time received for fruit ripening on experimental plants in Sri Lanka may have led to lower fruit:flower ratio estimates as plants can lose some fruits while ripening due to limitation of resources for fruit set or effects of predators and natural disasters.

We observed markedly low fruit set on experimental plants in the gorse population at Nuwara Eliya (Sri Lanka) which consisted of smaller plants compared to all other study sites due to recent clearance of the area. These immature plants could be too resource-limited to achieve higher levels of fruit set (e.g. Lawrence 1993).

Gorse populations in Sri Lanka are located at high elevations (>2000 m) whereas the elevation of gorse populations studied in South Australia vary from 200-500 m. Generally temperature decreases with increasing latitude and altitude. Precipitation increases can be observed in high latitudes, whereas in low latitudes it could be opposite (IPCC 2007). Therefore, gorse in Sri Lanka and South Australia experience different climatic regimes. Sutherland (1986) examined fruit set values for 447 species of plants for variation due to several variables (compatibility, breeding system, latitude, life form, type of pollination and type of fruit) and found latitude to be a significant predictor of fruit set among both self-compatible and self-incompatible plants. However, they concluded that latitude may not directly have a significant impact on fruit:flower ratio since it was correlated with some other variables they studied. This study also found that significantly higher fruit:flower ratios in temperate species compared with tropical species.

Seed production per pod

A gorse flower has 12 ovules (Bowman *et al.* 2008). A mature gorse pod contains a range of 1-12 seeds with an average of 4-5 seeds (Markin 2008). Our results suggest that gorse populations in Sri Lanka had a higher seed number per pod compared with gorse populations in South Australia. The level of seed production of a plant depends on the availability of pollen, pollinators in the environment, accessibility to resources and mortality of seeds or ovules by predation or some other factors (Agren and Willson 1992). Therefore, higher production of seeds in gorse population in Sri Lanka could be due to one or a combination of the above factors, which themselves may vary with time (Agren and Willson 1992). However, according to Hornoy *et al.* (2011), in their comparison study of several plant traits in native and introduced regions, the region effect was never significant for number of seeds per pod.

Blossey and Notzold (1995) supported the 'evolution of increased competitive ability' hypothesis which predicts exotic species can invest more resources for growth and reproduction and less resources for defence since they live in an environment free of natural enemies. The higher level of seed production in Sri Lanka may result from a relatively lower abundance of natural enemies but this aspect was beyond the scope of this study.

Simpson *et al*. (Simpson *et al.* 2005) report that a single bee on an average foraging day (6 hrs as an average foraging period per day) can result in the production of over 6000 seeds in scotch brooms (*Cytisus scoparius*). Since gorse and scotch brooms are ecologically quite similar species (Zielke *et al.* 1992), belong to the same sub-family and are both pollinated by honey bees, a high contribution of pollinators for seed production could be applicable for gorse as well. Contribution of pollinators in turn depends on visitation rate and quality of pollen (Karoly 1992) and intensity of pollinators in the study areas which are apparently not known. However, Gunatilleke and Wijayathilake (Somaweera *et al.* 2012) state that bees and several other pollinators visit gorse flowers.

Pod predation

Weevils and moths can cause destruction of 90% of gorse pods (Hill and Gourlay 1991; Atlan *et al.* 2010). Gorse seed predation due to the above predators varies with time of the year (Tarayre *et al.* 2007; Atlan *et al.* 2010). Hill and Gourlay (1991) state that oviposition by weevils in New Zealand occurs in spring and therefore, gorse pods produced before or after this period escape predation. Gorse may escape seed predation in two ways; by changing the time of fruit production before or after predators are active, or by producing massive numbers of fruits in a shorter period ((Hill *et al.* 2008); Atlan *et al.* 2010). We found few predated pods in our random samples from Sri Lanka but none from South Australia. Therefore, the levels of predator population were very low during our field visits in both countries and hardly sufficient to make an impact for gorse. According to a study done in the native range (Brittany, France), Atlan *et al.* (2010) found that ripe pods produced before June had no seed predators and then the pod infestation increased continuously. This study shows that genetic variation in gorse contributes to a high level of variation in seed predation by insects. Long term studies are needed to observe the changing pattern of predators over the year.

Predators may attack up to 90% of ripe pods resulting from spring flowering but are absent in pods resulting from autumn or winter flowering (Tarayre *et al.* 2007; Bowman *et al.* 2008). Since pod maturation of gorse takes about 3-4 months from pollination to dehiscence (Bowman *et al.* 2008), the ripe pods we observed in early spring in South Australia could be resulting from late autumn or early spring flowering. Therefore, our field sampling period could be too early to observe predators in South Australia. However, much less is known about the predator type, population size, impact and response to seasonal climatic differences. Therefore, long term studies are needed to observe the changing pattern of predators over the year.

The enemy release hypothesis which is one of the main accepted mechanisms of species invasion states that upon entry into a new range, invader losses its natural enemies that limit its population size in its native range (Keane and Crawley 2002; Catford *et al.* 2009). Since the level of predator population is very low in the new region, the species spread fast without control. Results of our study clearly indicate that the levels of predator populations of gorse were very low in both countries at least during one season. This condition may provide a favourable environment for gorse to spread fast and acquire a large area. Relaxation of Genetic Correlation (RGC) in introduced species, can enhance invasive potential by optimizing life history traits or by niche expansion (Hornoy *et al.* 2011).

The mortality of invasive species due to enemies in their invasive range is less than that in their native range due to the absence of specialist enemies in the new region (Keane and Crawley 2002). This has been used as the basis of biological control mechanism. According to above authors gorse seed weevil contributes 12-55% to mature gorse seed destruction annually in Tasmania. However, according to a computer modeling study done in New Zealand this level is not enough to make a significant impact to decline the gorse populations (Rees and Hill 2001).

Predation is potentially important in reducing the seed bank of noxious plants. Several researchers in New Zealand have investigated the effectiveness of gorse seed weevils in reducing the viability of gorse seeds. Cowley (2012) states that weevil attack reduced the viable seeds and remaining seeds in attacked pods failed to sprout in germination tests. Sixtus *et al*. (2003) found that 11% of gorse seeds that are attacked by the gorse seed weevil were viable and germinate successfully. During our gorse seed germination trials, we observed that seeds partly damaged due to scarification germinated well. Therefore, predators may have to damage gorse seeds fully (or a considerable portion) to stop seed germination.

Cowley (2012) states that gorse seed weevil larvae are active mainly in the spring and hence, gorse seeds set in autumn and winter escape predation. Ireson and Davies (2012) report that the gorse seed weevil is widespread in South Australia; however, during our field studies in early to mid-spring in South Australia, we did not observe predated gorse pods, perhaps due to variation in the timing of predator activity. In literature, we didn't find any records of pre-dispersal seed predators of gorse in Sri Lanka. Our results indicate that the predator active season in South Australia could be different or delayed relative to that in New Zealand.

The size of the seed bank

The information given in the literature on the distance that gorse seeds can be ejected after dehiscence is somewhat contradictory. According to Markin and Yoshioka (Markin and Yoshioka 1996), gorse seeds can be spread 1-3 m away from the parent plant. Moss (Moss 1959) stated that gorse seeds can be ejected about 5 m away from the parent plant. The above studies suggest that a boundary of around 5-6 m is needed to prevent infestations by ballistically dispersed seeds into neighbouring areas.

In our study, we found very few seeds in the seed bank 3 m away from shrubs in our study sites. However, we believe that other mechanisms such as seed dispersal by ants may potentially cause a greater spread of gorse seeds (Markin and Yoshioka 1996) several meters away (Gómez and Espadaler 2013). Hill *et al.* (2001) report that the majority of gorse seeds are deposited under the canopy with a higher concentration at the canopy margin. According to the above authors, seed fall gradually declines away from the margin and becomes very low at 3 m away from the parent bush. Our findings corroborate these results.

Even though the fruit : flower ratio is much less in Sri Lanka compared to South Australia and the pre-dispersal seed predation is negligible in both countries, there is a 50% higher density of seeds in the soil in Sri Lanka than in Australia. According to our experience the flowering intensity of gorse is quite similar in both countries. However, gorse is flowering year-round in Sri Lanka whereas in South Australia gorse flowers mainly in winter. Therefore, the number of flowers per unit area per year could be much higher for Sri Lanka relative to South Australia. The significant increase in number of gorse seeds in the upper layer of the seed bank in Sri Lanka relative to South Australia may be partly explained by the higher mean number of seeds in a gorse pod. It is possible that the production of many seeds in a pod could contribute eventually to increase the total number of gorse seeds in the seed bank substantially due to its fairly long lasting nature.

Ivens (1978) estimated over 10,000 gorse seeds per sq. meter in the seed bank in New Zealand. We estimated an average of 1419±211.95 and 2141±732.65 gorse seeds per sq. meter across our study sites in South Australia and Sri Lanka, respectively; however, we considered only the top layer (5 cm) of the seed bank, where approximately 75% of gorse seeds are contained (Hill *et al.* 2001). According to another study, the mean seed number was higher in the 5–10 cm soil layer than in the two other layers (0–5 and 10–15 cm) (Gonzalez *et al.* 2010). There are conflicting findings related to the changes in gorse seed bank density in different layers of soil. However, the total number of gorse seeds estimated in the 0-5 cm soil layer in our study is far higher than the numbers the above authors found in the native context (66.3 to 385.9 per m^{-2}, table 01).

The gorse seeds we extracted from the seed bank ranged in colour from yellow, yellowish green, olive green to reddish brown, brown to black. The different colours of the seeds could possibly provide an idea of the age of seeds in the seed bank. Yellow and green seeds, which look quite fresh and shiny, could be the most recently deposited whereas black seeds that are somewhat shrunken and small in size could be much older. We observed many green, fresh seeds compared with few black seeds in the soil seed bank. Moss (1959) reported that gorse seeds can stay in the soil seed bank about 28 years (see also Markin and Yoshioka (1996)). However, based on our findings, we believe that only a certain portion of gorse seeds can persist for a long time in the soil seed bank.

Gouldthorpe (2006) mentions that most of the gorse seeds recovered from the soil seed bank are viable which was similar to what we observed during the study. Some gorse seeds needed to be scarified before germination due to their hard seed coat. We noticed that scarified seeds had much more rapid germination than non-scarified seeds. We found that altogether around 91% of seed bank gorse seeds germinated before and after scarification which was higher than that seen following the acid scarification of hand-picked gorse seeds (81%) done by Sixtus *et al.* (2003).

However, under the given statistical similarities and differences above, the results must be interpreted carefully as the data collection was done in a specific period of the year. The differences encountered could be due to seasonal effects of the year that we collected data and the results may not have captured long-term fundamental differences.

Conclusion

Several aspects contribute to the success of gorse in its invasive range. The findings of this study reveal that the contributions of traits that influence the reproductive success of gorse could vary among countries in the invasive range. The results we obtained for fruit:flower ratios and seed predation are more tentative since differences in seasonality were not adequately captured and hence further studies are needed. The seed bank density drastically reduces 3 m away from the parent bush, suggesting a minimum level of boundary demarcation needed for a conservation action in gorse-affected areas. These findings provide some baseline information for managers to design programs for control of gorse.

ACKNOWLEDGEMENTS

We would like to thank the Department of Environment and Natural Resources, Government of South Australia and Department of Wildlife conservation, Sri Lanka for granting permission to conduct field works within the State's system of conservation reserves. The State Herbarium of South Australia is gratefully acknowledged for providing geo-referenced gorse (*Ulex europaeus*) herbarium data.

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Table 1 Comparison of findings of the present study with native range data.

Trait	Findings of present study	Comparison with native range	Reference	Study site
		Similarities / differences		
Fruit set and fruit: flower ratio	Fruit: flower ratio was higher in South Australia (0.85) compared with Sri Lanka (0.26)	In winter Fruit: flower ratio was 0.43 and in spring it was 0.72	(Bowman *et al.* 2008)	Rennes, Brittany, France
Seed production per pod	2.9 seeds per pod in South Australia and 3.7 seeds per pod in Sri Lanka.	Seeds per pod in the population is 1.7	(Atlan *et al.* 2010)	Brittany, France
		Winter flowering pods contained more seeds. Winter pods produced an average of 3.07 ± 0.6 seeds per pod whereas spring pods produced an average of 2.93 ± 0.5 seeds per pod.	(Bowman *et al.* 2008)	Brittany, France
		Coastal populations produced significantly more seeds (approx. 2.9) per uninfested pod than inland populations (approx. 1.6)	(Barat *et al.* 2007)	Brittany, France
	In South Australia a range of 1-8 seeds in gorse pods whereas the range was 1-12 in pods in Sri Lanka.	The numbers of seeds per uninfested pod varied from 0 to10	(Barat *et al.* 2007)	Brittany, France

		0% in winter pods and 68% in spring pods	(Bowman *et al.* 2008)	Brittany, France
		Proportion of infested pods of inland populations was higher (66%) than for coastal populations. (34%).		
The size of the seed bank	The density of gorse seeds in the top 5 cm layer of the soil showed a marked increase under gorse shrubs compared with that 3 m away from shrubs (19 times higher in South Australia and 8 times higher in Sri Lanka) Density of gorse seeds in the 0–5 cm soil layer of the seed bank under shrubs in Sri Lanka (2141±732.65 seeds/m^2) was 1.5 times higher than that of South Australia (1419±211.95 seeds/m^2)	Mean seed number per m^{-2} with standard error, in the 0–5 cm soil layer varied from 66.3 to 385.9. The total mean number of seeds in all 3 layers (0-5 cm, 5-10 cm and 10-15 cm) varied 503 - 1312 seeds m^{-2} The mean seed number was higher in the 5–10 cm soil layer than in the two other layers (0–5 and 10–15 cm)	(Gonzalez *et al.* 2010)	South-western France

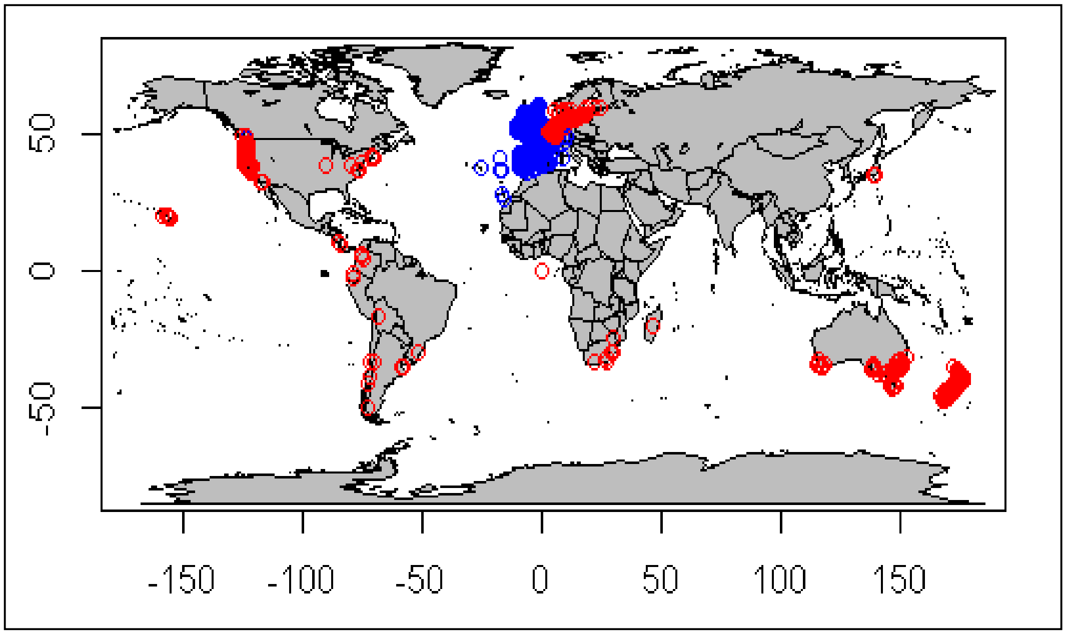

Fig. 1 Occurrences of gorse (*Ulex europaeus*) in the world; the native range is shown in blue and the introduced range is shown in red

(The above map was prepared using the *Ulex europaeus* location information available on-line at the Global Biodiversity Information Facility data portal (http://www.gbif.org/), virtual herbaria of Australia (http://avh.ala.org.au) and New Zealand (http://www.virtualherbarium.org.nz) and data received from Dr. James Leary, University of Hawaii at Manoa).

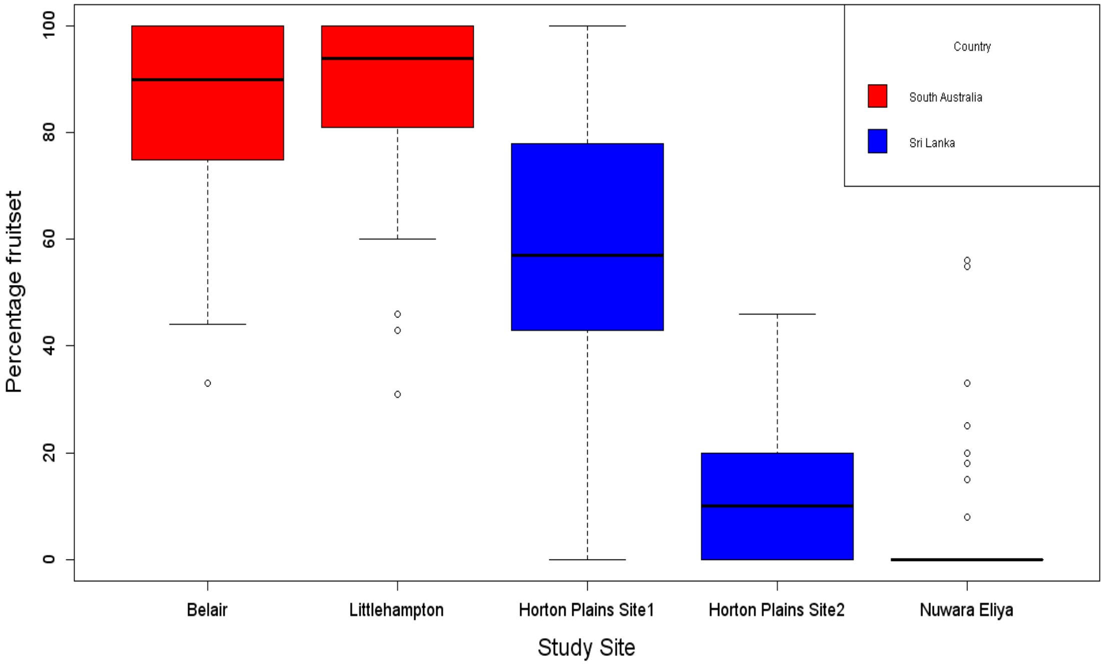

Fig. 2 Percentage fruit set (fruit to flower ratio*100) of gorse (*Ulex europaeus*) across study sites in South Australia and Sri Lanka

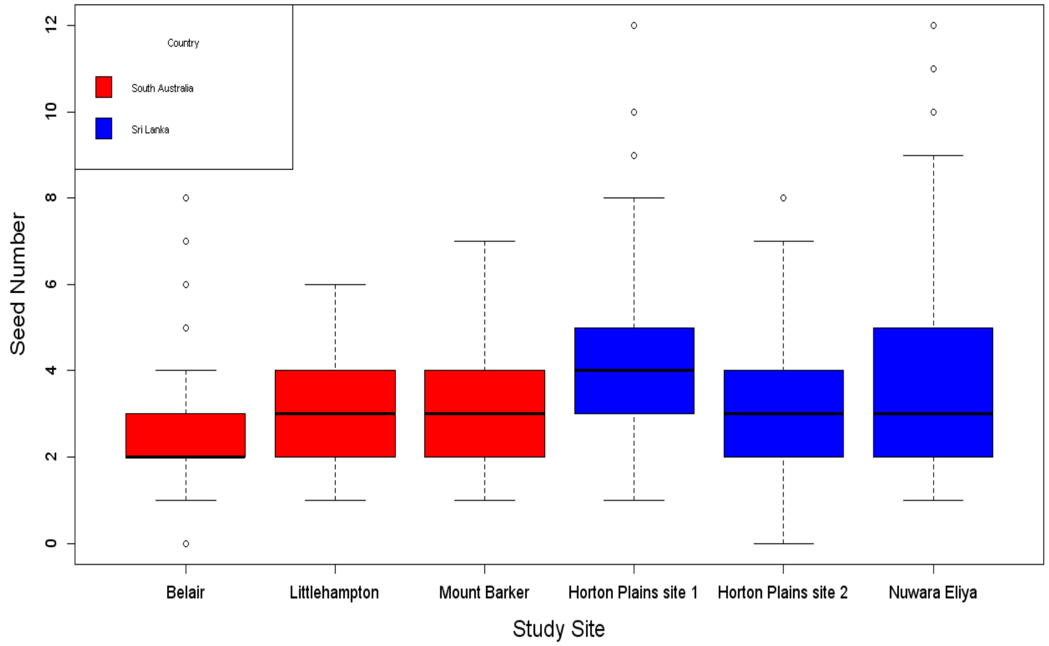

Fig. 3 Number of seeds per pod in gorse (*Ulex europaeus*) in the study sites in South Australia and Sri Lanka.

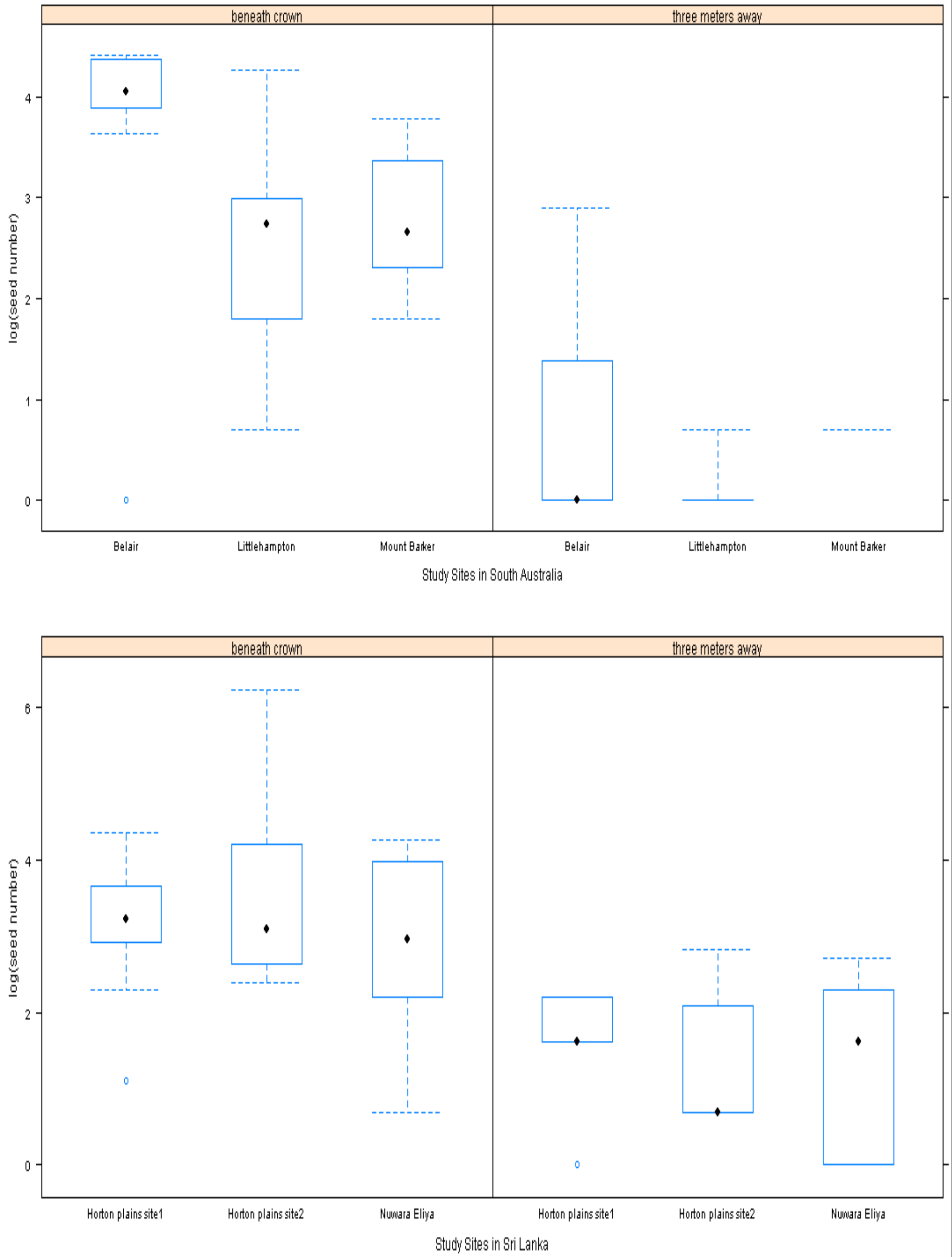

Fig. 4 Number of seeds in top 5 cm layer of soil seed bank (log value) against each study site in two locations (under shrub and 3 m away the shrub) in South Australia and Sri Lanka

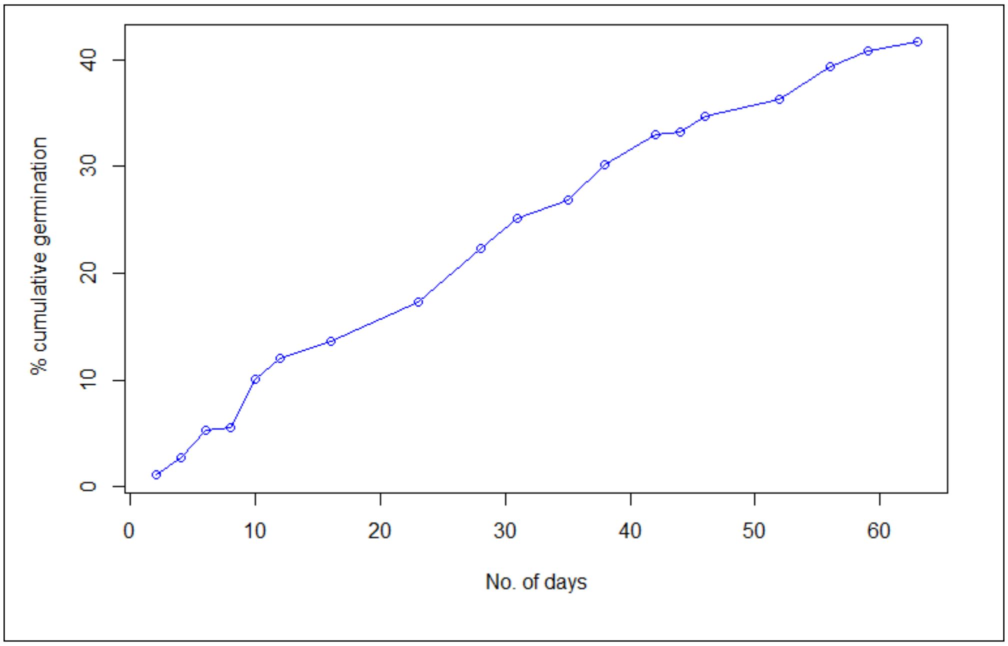

Fig. 5 Germination pattern of seed bank gorse seeds in South Australia

Chapter 3

Comparative study of the invasive ranges of gorse (*Ulex europaeus*) in the Mount Lofty Ranges of South Australia and central highlands of Sri Lanka using species distribution modelling

Champika S. Kariyawasam, Duncan A. Mackay and Molly A. Whalen

B.Sc(Hons), M.Sc

Flinders University, School of Biological Sciences, GPO Box 2100, Adelaide, SA 5001, Australia

Kariyawasam, *et al*. (unpublished)

Key words: invasive species, Maxent, species distribution modelling, *Ulex europaeus*,

ABSTRACT

The distribution of gorse (*Ulex europaeus)* plants in South Australia has been modelled using 126 presence-only location data as a function of seven climate parameters. The predicted range of *U. europaeus* is mainly along the Mount Lofty Ranges in the Adelaide hills and on Kangaroo Island. Annual precipitation and yearly average aridity index appeared to be the highest contributing variables to the final model formulation. The Jackknife procedure was employed to identify the contribution of different variables to gorse model outputs and response curves were used to predict changes with changing environmental variables. Based on these analysis, we revealed that the combined effect of one or more variables could make a completely different impact to the original variables on their own to the model prediction. Our work also demonstrates the need for a careful approach when selecting environmental variables for projecting correlative models to climatically distinct area. We found that Maxent acts as a robust model when projecting the fitted species distribution model to another area with changing climatic conditions, whereas we found GLM, Bioclim and Domain models to be less robust in this regard. These findings are important not only for predicting and managing invasive alien gorse in South Australia and Sri Lanka but also in other countries of the invasive range.

INTRODUCTION

Usefulness of species distribution models to predict the spread of invasive species

An understanding of current and potential distribution patterns is fundamental for managing invasive alien species (Ward 2007; Gormley *et al.* 2011). Preventing alien species invasion is hampered due to difficulties in predicting possible areas of invasion in space and time (Gertzen and Leung 2011). In this context, identification and recognition of effective methods and techniques to assess species distribution patterns are important in conservation planning (Baldwin 2009). Species Distribution Modeling (SDM), the prediction of species' geographic distributions based on environmental variables and available records of species occurrence, is an increasingly used technique (Graham and Hijmans 2006; Phillips *et al.* 2006; Glor and Warren 2010). This technique has provided much needed information about species ranges (Glor and Warren 2010) for conservation planning and related applications.

SDM is commonly used to predict the likelihood of species occurring in unsurveyed habitats such as remote and inaccessible areas (Pearce and Ferrier 2000; Franklin 2009); or to predict the potential geographic range of species whose current distribution is thought to be in a non-equilibrial state. The resulting predictive maps have the potential for use in various scientific applications related to resource management and conservation planning such as biodiversity assessment, reserve design, habitat management and ecological restoration, assessing potential threats of invasive species, identifying hotspots of endangered species, and identifying suitable habitats for species translocations (Beaumont *et al.* 2005; Phillips *et al.* 2006; Franklin 2009).

Ecological theories and assumptions, e.g. the species niche concept, underpin many SDMs (Guisan and Zimmermann 2000; Guisan 2005). Hutchinson defined the niche as n-dimensional hyper-volume within which a species can survive and reproduce; in the absence of biotic interactions this volume is equal to the species' fundamental niche (Franklin 2009). However, under a given circumstance, a species will usually only occupy a certain part of the fundamental niche, which is called the realized niche (Jimene-Valverde *et al.* 2011). Therefore, theoretically, SDM estimates a species' potential distribution rather than the actual distribution. When the species niche is projected to a geographical space, it yields a predictive map of species' presence (Phillips *et al.* 2006; Tsoar *et al.* 2007). These predictions distinguish suitable habitats from unsuitable habitats in the study area (Gormley *et al.* 2011). In some models, a threshold value can be used to transform a continuous probability of occurrence into a prediction of either presence or absence (Liu *et al.* 2005). The predicted area where conditions are suitable for the survival of the species is often called the species' 'potential distribution' while the actual area occupied by the species is called the species' 'realized distribution' (Phillips *et al.* 2004).

In SDM, inappropriate use of environmental parameters can lead to erroneous predictions (Beaumont *et al.* 2005); therefore, identification of suitable environmental parameters is an important step. The amount of locational data required for niche modelling is not well understood and is highly dependent on the distribution of available data and the environmental variability of the study area (Glor and Warren 2010).

Modelling methods are typically based on several assumptions. In SDM, it is assumed that species are at equilibrium with the environment or the species has already acquired all suitable habitats (Elith and Leathwick 2009; Elith *et al.* 2010; Sinclair *et al.* 2010; Gallien *et al.* 2012). However invasive species could deviate from this assumption and therefore, the applicability of SDMs for predicting the distribution of invasive species could be controversial (Gallien *et al.* 2012). How the non-equilibrium nature of the distribution of invasive species affects the model prediction and at which level is not well understood (as discussed in Vaclavik and Meetemeyer 2012). These limitations may lead to imperfect predictions of species invasion (Thuiller *et al.* 2005). In some cases, full occupancy of a species' potential range is hindered due to geographic barriers, species interactions, behavior, and lack of time for colonization (Elith 2000; Anderson *et al.* 2002; Anderson 2003; Franklin 2009; Hortal *et al.* 2010). Often the estimated extent of all suitable habitat (both occupied and unoccupied) of an invasive species is larger than the actual area occupied by the species (Ward 2007; Vaclavık and Meentemeyer 2012).

A variety of statistical approaches are currently in use for the development of SDMs (Graham and Hijmans 2006; Franklin 2009). The selection of a specific model for a certain application basically depends on the model performance (Guisan and Thuiller 2005; Barry and Elith 2006). Model performance could be tested across multiple methods to select the best model for a specific application; however, model comparisons are not informative without an explanation for those models that show improved model performance (Elith and Graham 2009). Theoretically, the accuracy of model performance can be enhanced by improving the model complexity with more relevant data (Webber *et al.* 2011). The selection of a modelling technique could be a choice of the researcher based on available data and intended application; however, this requires good knowledge of various modelling methods (Elith and Graham 2009). Criteria and guidelines for model selection are not yet formally developed and a comprehensive guidance is still lacking for the selection of the best modelling method for a particular SDM application (Elith and Graham 2009). In this context, the selection of modelling method mostly depends on the access to modelling software and knowledge of modelling techniques (Elith 2000). This situation may lead the modeller to select his or her ‘pet model’ rather than the ‘best model’, possibly reducing the reliability of the SDM.

Few studies involve meaningful comparisons of modelling methods for SDM (Elith 2000; Tsoar *et al.* 2007). Elith (2002) compared the performance of several modelling methods for predicting the ranges of seven Australian plant species and found that none of the models performed significantly better than the others across the modelled species. Elith, Graham *et al*. (2006) did a comprehensive analysis to evaluate the influence of presence-only occurrence data on the predictive accuracy of species distribution models. They compared 16 modelling methods over 226 species from six regions in the world and found that novel modelling methods like Maxent out-performed more established modelling methods.

Webber, Yates et al (2011) conducted a comprehensive study to explore the global distribution pattern of *Acacia cyclops* and *A. pycnantha* using two correlative models (Maxent and Boosted Regression Trees) and one mechanistic niche model (Climex). They fitted the above three models using two training data sets, native-range data (Australian data) and global data (excluding South African records) and compared the ability of the models to project the climate suitability for observed records in South Africa for the above two species. They observed significant variation in the projected range limits. They also assessed the potential impacts of novel climates on the distribution of these species in their native and invasive ranges. This work illustrates a need for a cautious approach when projecting models under climate change scenarios, especially with invasive species.

The Maximum - entropy algorithm or Maxent software (Phillips *et al.* 2006) is one of the more accurate, increasingly popular and globally accepted machine-learning techniques currently in use (Graham and Hijmans 2006; Ramirez-Villegas and Bueno-Cabrera 2009) for presence-only data (Baldwin 2009). It estimates the probability distribution of maximum entropy of each environmental variable across the entire study area (Graham and Hijmans 2006). Maxent performs extremely well in predicting distributions of species across landscapes compared to other popular approaches for presence-only data (Elith *et al.* 2006). Even though, Maxent has received a huge recognition worldwide, it has recently been shown to be exactly mathematically equivalent to a GLM poisson regression model which is an older statistical model (Renner and Warton In press). Recent research has shown that models with presence-only data are accurate enough for SDM studies (Elith and Leathwick 2007; Ward 2007).

Geographically referenced herbarium records are a valuable source for SDM studies based on presence-only data.

Maxent has been used for a range of applications for varying purposes, extents and species (Elith *et al.* 2011). The majority of Maxent studies focus on predicting the potential distribution of a study species, such as exotic plants (Crossman *et al.* 2011); invasive sambar deer (Gormley *et al.* 2011); Australian *Acacia* species (Webber *et al.* 2011); invasive fruit fly, *Bactrocera invadens* (Meyer *et al.* 2010); cassava green mite, *M. tanajoa* (Lu *et al.* 2012); Argentine ant, *Linepithema humile* (Roura-Pascual *et al.* 2009); and the space-weaving spider, *Chibchea salta* (Rubio and Acosta 2011). Interestingly, Maxent model has been used for identifying helicopter-landing suitability based on available geographic data (Doherty *et al.* 2012).

There are several other well-established modelling techniques to predict the potential distribution of species. Bioclim (Nix 1986) is a climate mapping approach which uses species presence data and climate variables to form a 'climatic envelope' for the species (Elith 2000). In this envelope, the 5–95th percentile of the volume is marked as a 'core' regions of suitability for the species (Ward 2007). The Bioclim program produces ranked predictions for each site of interest, which define the climatic suitability of the habitat for the species (Elith 2000; Hernandez *et al.* 2006).

Domain (Carpenter *et al.* 1993), which also uses data on the presence of species, does not develop climate bounds as in Bioclim; but it identifies environmentally similar sites using a distance-based method (Elith 2000; Elith *et al.* 2006; Ward 2007). Domain produces a point-to-point similarity metric to assign a value to a potential site where higher values are considered "highly suitable" (Hernandez *et al.* 2006; Ward 2007). Bioclim and Domain are relatively simple species locality and environmental data matching models but model complexity increases in Maxent or Generalized Linear models (Elith and Graham 2009). In generalized linear modelling (GLM), predictor variables and a response variable are related by a link function to fit the model (Elith 2000). Logistic regression and Poisson regression are among the popular GLM types for SDM (Elith 2000). Logistic regressions have been used widely to predict the habitat use of species in conservation planning because of their robust statistical foundation (Pearce and Ferrier 2000; Austin 2002) .

Generally SDM studies use two types of data for model construction, presence-only data and presence-absence or background data. The vast majority of freely available data are presence-only and these data have inherent limitations for use in SDM studies (Zaniewski *et al.* 2002). Presence-only data indicate only locations that are environmentally suitable for a species, whereas presence-absence data also indicate the opposite (environmentally not suitable locations for a species) with more information (Lobo *et al.* 2010). The above authors define three kinds of absences that are due to unfavorable environmental conditions, dispersal limitations (environmentally favorable) and methodological absences (due to incomplete and biased distributional information). Models that use presence –only data use only occurrence data disregarding the range of environmental conditions available to species in the region which can be obtained by a sample of points in the study region (Phillips *et al.* 2009). These points which are considered as background data is not a substitution for absence data, but they provide a sample of set of environmental conditions (Phillips *et al.* 2009) specific to the species and chosen uniformly at random from the study area (Phillips *et al.* 2009). Bioclim and Domain (profile methods) only consider presence-only data whereas GLM (regression models) considers presence-absence data. Maxent (machine learning models) uses presence-background data.

Recently, SDM has been recognized as an important and powerful tool to assess the invasion risk of species before they are introduced to a new habitat (Thuiller *et al.* 2005). The latter authors developed SDMs using generalized additive models (GAM) for 96 endemic plant taxa that are known to be invasive in other countries, evaluated and subsequently projected over the world for three important invasive species. They found a close match between habitat suitability and actual occurrence of these species worldwide, suggesting that SDM models are useful to identify geographic areas susceptible to species invasion.

Elith, Kearney et al. (2010) predicted the current and potential distribution of the invasive cane toad (*Bufo marinus*) in Australia using four different modelling techniques, three regression type models (Generalized linear model, GAM and Boosted Regression Tree) and Maxent. The authors observed that the predictions vary with the modelling method used and that models that performed similarly under current climate conditions showed significant differences under alternative climate change scenarios.

Ulex europaeus L. (Fabaceae), popularly known as gorse, is a native of Europe (Parsons and Cuthbertson 1992; Markin and Yoshioka 1996; Ireson *et al.* 2008; Atlan *et al.* 2010;

Ireson and Davies 2012) and the British Isles (Hill *et al.* 2001). Gorse is a non-destructive and commercially important plant in its native range but it behaves as a notorious invader in most of its exotic range (Atlan *et al.* 2010). It is a nuisance weed in more than 15 countries in the world (Markin and Yoshioka 1996).

Since gorse is an invasive species we would like to model its distribution in two geographic areas in its invasive range, South Australia and Sri Lanka, where the species might not yet have occupied all available suitable habitats of the environment. Gorse is an interesting species for SDM due to its long history of establishment in its invasive range and especially in South Australia, the availability of a large number of records in natural history collections and its ecological and economic importance.

There are few other attempts to predict the potential habitat suitability of gorse in native and invasive ranges. Baret *et al*. (2006) derived environmental suitability surfaces for gorse based on the Mahalanobis Distance in La Reunion Island. They used slope other than climatic factors (precipitation and temperature) for the modeling and generated a predictive map of species distribution over the whole island. This study revealed that invasive species like gorse may have a large potential range and could invade substantial additional area currently remaining as natural habitat. Fernandez *et al.* (2012) compared performance of Maxent model using the area under the curve (AUC) of the receiver operating characteristic plot for 10 invasive species including gorse in their native and invaded ranges. In this study, SDMs showed significant improvement in performance for gorse in the invasive range. Retuerto and Carballeira (2004) characterised the climatic behaviour of 53 woody species including gorse in Spain, in terms of the climatic factors that play the main role in controlling species distribution in the study area. They tested the species' climatic behaviour by different methods and found out that species such as, *U. europaeus* had extremely high climatic position (the mean position of a species along a climatic gradient, normalised with respect to the position of the other species considered) for the selected climatic factor, Baudiere's *Qe* drought index. In general, a species with high climatic positions are considered as best indicator taxa that can be used for environmental monitoring.

Aims

The aim of this study is to understand the species distribution pattern of invasive alien gorse species in the Mount Lofty Ranges in South Australia and possible range expansion of gorse in Sri Lanka to provide suitable recommendations for land managers. In this study we are aiming to;

(i) Use data on the current distributions of gorse in South Australia to predict the potential range of this species in South Australia, and to

(ii) Predict the potential range expansion of gorse in Sri Lanka

METHODOLOGY

There are many methods for modelling the spatial distribution of a particular species. The potential distribution of *Ulex europaeus* under current climates was explored using

Maxent software (version 3.3.3k). We used herbarium data for the present study which are not always sufficiently precise for distribution modeling. These data, which have been compiled over many decades, were collected for a variety of purposes and not just for delimiting species ranges. Under these conditions, the modeling success of any single method was not certain. There was a tendency that Maxent model perform slightly better than the other models, however, model performance may change with the species being modelled and the subset of predictor variables used. A comparative study of model prediction was conducted with several well-known modelling algorithms, GLM, Bioclim, Maxent and Domain in the 'dismo' (Hijmans *et al.* 2013) package in R program (R Development Core Team 2012) since these modeling methods have produced useful predictions in previous research studies.

Species distribution modelling with Maxent software for *Ulex europaeus* in South Australia

Species Distribution Data

A database of locality data was obtained from the State Herbarium of South Australia, Adelaide. Records with precise data were filtered. Precision level is an indicator of the accuracy of location information / geocode, as interpreted by the person entering the data into the specimen database; if the level is 1 or 0.5, the location is considered very accurate while 4 indicates that the location is very general (H.Vonow, 2013, email, 19 August). Our data represented 154 presence-only records from a 75-year period (from 1936 to 2011) of specimens held in herbaria in South Australia. The specimens data are from collections made by various individuals including professional scientists, amateur botanists and members of the public. Most of the records included geographical coordinates, locality data, determiner's name, date of collection, state and region.

In Sri Lanka, all available gorse locational records were taken during the field study period (Table 1), as we did not locate any previous geo-referenced records for Sri Lankan gorse in local or international herbaria.

The occurrence records were stored in comma-separated value (.csv) file format. Records with incomplete latitude and longitude information were deleted. The location data were converted to decimal degree (DD) format as species data should be in the same coordinate system with environmental data. Duplicate records were removed using 'exact match' option of the ENM tools (Warren *et al.* 2010). Data cleaning reduced the number of available records resulting to a final set of 126 geo-referenced records.

In the models we used that considered presence-absence data, 'assumed absences' or 'pseudo-absences' were used (i.e. random locations in the species' range where it had not been recorded from) as absence data. Pseudo-absences were selected randomly from all points within the studied area.

Environmental data

Identification of appropriate variables for a modelling exercise is challenging (Franklin 2009). According to the literature, climatic variables, especially temperature and rainfall, play a major role in determining the distribution of gorse species (Richardson and Hill 1998).

During our pilot studies, Maxent model was run with 19 bioclimatic variables given in the WorldClim (http://www.worldclim.org/) web site and allowing the model to select highly contributing variables. These trials indicated that bioclimatic variables which are derived from monthly temperature and rainfall values generate biologically meaningful parameters. In Maxent, the model gain which is assigned to an environmental variable increases at each step of the algorithm. At the end of model run, these values are converted to heuristically defined percentage values (Phillips 2010). Therefore, the highly contributing bioclimatic variables for model prediction were selected for our study. Variable response curves and jackknife results generated by Maxent also showed that the selected variables (Table 2) are strong predictors. The selected variables were supplemented with 'yearly average aridity index' since this parameter showed a strong impact on the model prediction. The aridity index is a function of precipitation and temperature and it has been used to quantify precipitation deficit over atmospheric water demand (Zomer *et al.* 2008). We felt that the selected subset of variables (Table 3) captures key biophysical features of gorse species since they represent basic parameters of insolation, water availability and temperature.

The selected environmental rasters were downloaded from the Worldclim database (Hijmans *et al.* 2005), version 1.4 (http://www.worldclim.org/). They were based on current (1950-2000), high resolution (30 arc-seconds (~1 km^2)), tiled (410 and 28 tiles) data. Global aridity index data were extracted from CGIAR-CSI website (http://www.cgiar-csi.org) (Zomer *et al.* 2007; Zomer *et al.* 2008). Environmental data were re-sampled for the South Australian geographic area of prediction representing the Mount Lofty Ranges, Kangaroo Island and York and Eyre Peninsula (134.2917ºE, 140.5ºE, -36.10833ºS, -32.2ºS) and for the Sri Lankan extent representing Tamil Nadu, Kerala and Sri Lanka (73.99817ºE, 83.00615ºE, 4.99167ºN, 12.99968ºN). All Raster layers were checked to ensure all files had the same extents and resolutions.

After exploratory modelling, we selected a subset of seven highly contributing variables (Table 2) which included "annual mean temperature" (=bio1), "isothermality" =bio2/bio7 * 100 (=bio3), "max temperature of warmest month" (=bio5), "mean temperature of warmest quarter" (=bio10), "annual precipitation" (=bio12), "precipitation seasonality (coefficient of variation)" (= bio15), and "yearly average aridity index" (= res_ai_yr). Pearson correlations among variables were tested using ENM tools, version 1.3 (Warren *et al.* 2010).

Settings for Running the Model in Maxent

The Maxent Maximum Entropy Modelling software package version 3.3.3k was employed for the study (Phillips *et al.* 2009). We selected the "Do Jackknife to measure variable importance", "create response curves" and "make pictures of predictions" options. The cumulative output format instead of the default logistic output was chosen. The random test percentage was set to 25% for both species enabling the model automatically to allocate all presence points into training (75%) and test (25%) samples.

Other relevant default settings of the Maxent software were applied, including the maximum number of background points (10,000), replicated run type (crossvalidate), maximum iterations (500), convergence threshold (0.00001), and default prevalence (0.5). Auto features were activated.

The model was run several times changing the feature types, test percentages and number of maximum background points and the resulting output html files were checked for comparison.

The resulting asc file (one of the outputs of Maxent) was imported in the program “DIVA-GIS” to create a binary presence-absence raster map of potential distribution areas (Scheldeman and Van Zonneveld 2010). The resulting presence-absence predictions were visualized based on the selected threshold value.

The Maxent model built using South Australian gorse data was projected to the whole of Australia. The relevant output asc file from Maxent was imported to DIVA-GIS and a binary presence-absence map was made at a 10 percentile training presence. All available locality data of gorse in Australia were overlaid on the image to test the prediction.

Maxent projection to Sri Lanka using Maxent software

The aim of this task was to project the Maxent model for gorse that we fit to data from South Australia to the Indian sub-continent. The same seven environmental variables were used as projection layers. The relevant output asc file from Maxent was imported to DIVA-GIS and a binary presence-absence map was made at a 10 percentile training presence. The available few locality data of gorse in Sri Lanka were overlaid on the image to test the prediction.

Multiple SDM model comparisons for *Ulex europaeus* in South Australia

The ‘R’ statistical program (R Development Core Team, 2012) which is free open source software, facilitates SDM together with packages such as ‘dismo’ (Hill and Gourlay 1991) and ‘raster’ (Hijmans and van Etten 2013).

Four different species distribution modelling methods, namely GLM, Bioclim, Domain, and Maxent, were run in the R version 2.14.2 statistical programming environment using packages ‘dismo’ (Hijmans *et al.* 2013), ‘raster’ (Hijmans and van Etten 2013), ‘rJava’ (Urbanek 2013) and several model functions in R to compare the potential predicted distribution among modelling algorithms. The aim of this exercise was to investigate the relative ability of different algorithms to make predictions under current climate and to compare the robustness of predictions between these modelling techniques. The same environmental data layers (previously used in Maxent) were used in raster (grd files) format and the same gorse occurrence data were used. Models fit under each of the above modelling techniques were evaluated and predicted for South Australia. Maps of predicted presences and absences were generated under each model for a given threshold.

Algorithms were run several times changing the partition testing and training sets of the data and changing the number of background points. In each case, model predictions were compared across different modelling techniques based on the area under the ROC curve (AUC) which is a threshold independent measure of overall accuracy of the model (Phillips *et al.* 2006). AUC value ranges from low value (0) to a high value (1), where a value of 1 indicates the model perfectly identifies presence and absence points and a value of 0.5 indicates the model performs no better than random or has no predictive power (Boyce *et al.* 2002; Graham and Hijmans 2006; Gormley *et al.* 2011).

SDM model projection to Sri Lanka in 'dismo' for *Ulex europaeus*

We tried to carry out a multiple model comparison for the projection of *Ulex europaeus* to the Indian sub-continent in 'dismo'. To accomplish this task, all four modelling techniques described above, GLM, Bioclim, Domain, and Maxent were individually used. The four models, that fit in 'dismo' to South Australia were projected to the Indian sub-continent (73.99817, 83.00615, 4.99167, 12.99968) for prediction of gorse available areas in Sri Lanka.

Comparison of values of environmental variables in South Australia and Sri Lanka

The range of all cell values of all seven environmental variables used in the modelling task in South Australia and Sri Lanka were compared. 'GetValues' function in 'raster' package was used to return all cell values of the environmental raster layers.

RESULTS

Species distribution modelling with Maxent software for *Ulex europaeus* in South Australia

The final Maxent model prediction (cumulative output) is shown in Figure 1. In this figure values scale from 0.00001 (totally unsuitable) to 100 (maximum suitability) as denoted by a color-coding ranging from blue to red. Warmer color areas (red) are the areas with a high probability for the presence of gorse. Yellow areas are the areas where the conditions are suitable for the species to be present. Green areas show less predicted suitability for the species to be present while the prediction is minimal in blue areas (Phillips 2010). The Mount Lofty Ranges and Kangaroo Island areas are predicted as high probability areas for gorse where the majority of training (white dots) and test (violet dots) samples are distributed. However, parts of Yorke and Eyre Peninsula and southern coastal areas are also predicted as suitable for gorse, and we had only a few gorse herbarium records from the Yorke Peninsula, and none from the Eyre Peninsula. Nonexistence of herbarium records in Eyre Peninsula does not indicate absence of the species there; in fact, several web sites record the presence of gorse in lower Eyre Peninsula (Adelaide & Mt Lofty Ranges Natural Resources Management Board 2010). G. Marshall confirmed this by email on 19 March 2015.

Figure 2 shows how testing and training omissions and the predicted area for gorse vary with an increasing cumulative threshold. In the graph the omission of training samples and omission of test samples are quite close and parallel to the predicted omission indicating that test and training data are independent (Phillips 2010).

Figure 3 shows the receiver operating curve (ROC) for both training and test data of the final *U. europaeus* model. The red (training) and blue (testing) lines show the "fit" of the model to the training and testing data respectively. The blue line is an indication of the model's predictive power; in this model the blue line falls towards the top left corner of the graph which means that the model predicts presences of the test sample better (Phillips 2010). According to the graph, the model was found to have a high predictive power or good discrimination ability, with very high AUC values of $AUC_{training}$= 0.974 and AUC_{test}= 0.982 (Fielding and Bell 1997; Araujo *et al.* 2005).

Table 3 shows how various thresholds can be used in Maxent to limit the potential distribution of *U. europaeus*. This table lists different criteria for selecting cumulative and logistic cutoff values that differentiate suitable and unsuitable areas of the predicted map. The resulting output file from the Maxent model was imported to the DIVA-GIS program and the predicted area visualized at 10 percentile training presence where the cumulative threshold is 12.295 (row 5 of table 2). All areas greater than this threshold were predicted as areas where *Ulex europaeus* is predicted to occur under current climate conditions. The gorse location data were overlaid on this predicted area and all points fell within the predicted area (Fig. 4). The predicted range lies mainly along the Mount Lofty Ranges in the Adelaide hills and Kangaroo Island areas. The predicted range of gorse under this threshold does not include the Eyre Peninsula but does include small scattered areas of the York Peninsula. However, a greater predicted area, comprising all of the York Peninsula and a considerable part of the Eyre Peninsula would be observed using the threshold derived from the Minimum training presence where the cumulative threshold value is 0.753 (row 4 of table 2; Fig. 5).

The contribution of different variables to the overall model prediction was also analyzed. Table 3 provides two assessments of the relative contributions of the predictor variables to the Maxent model. Annual precipitation (bio12) and yearly average aridity index (res_ai_yr) appeared to be the highest contributing variables for the model formulation under the "percent contribution" criterion. These are the most dominant variables at each model run with different random test percentages and background points. These variables also differ in their contribution under the permutation importance criterion. Figure 6 shows a plot of the raster stack of seven predictor variables used for the *U. europaeus* model in South Australia. Each small map in this plot illustrates how the values of that variable vary over the area of prediction. Exploration of each of these maps implies a close relationship with the Maxent prediction. The highly contributing variables to the Maxent prediction (Table 3), annual precipitation (bio12), yearly average aridity index (res_ai_yr) and annual mean temperature (bio1) show quite similar patterns on these maps as did the final Maxent prediction.

Since these variables can be correlated the relative contribution of each variable should be interpreted carefully (Phillips 2010), and according to Pearson correlation analysis, annual precipitation (bio 12) and yearly average aridity index (res_ai_yr) variables are highly correlated (r = 0.97), therefore, the importance of these variables may be an overestimation. Pearson correlation analysis also revealed that annual precipitation (bio

12) and annual mean temperature (bio 1) are fairly correlated (r = 0.715). Therefore, it is hard to say that annual mean temperature is not important to the model, even though Maxent has used this variable least out of all the seven predictor variables.

Jackknife tests of variable importance were also used to evaluate the contribution of each environmental parameter to the predicted distribution of gorse (Fig. 7). Annual precipitation (bio 12) appeared to be the environmental variable with the highest gain when used in isolation in all three jackknife plots. Thus, it provides the most useful predictive information by itself. This was followed by yearly average aridity index (res_ai_yr), annual mean temperature (bio 1), and mean temperature of the warmest quarter (bio10). Yearly average aridity index (res_ai_yr) and annual precipitation (bio12) that contributed strongly to the model (Table 4) are the most important variables in all three jackknife tests too. We found that isothermality (bio3) achieves little fit in jackknife training, test and AUC plots; however, it was a relatively important variable in the final model (Table 4). Isothermality (bio3) appeared to be an environmental variable that decreases the gain the most when excluded from the model. Thus, this variable provides the most useful information that is not present in other variables. The model was run again removing isothermality (bio3), but this reduced both AUC and model gain; hence, isothermality (bio3) may contain unique information which is not common to the other variables and hence should be retained as a predictor of the distribution of gorse in this environmental regime.

The order of variable contribution to jackknife training gain, test gain and AUC (Fig. 7) was the same in all three jackknife plots; however, the magnitudes were slightly different. The variables that had a high gain for the training data also give similar results on the set-aside test data as well (Fig. 7 (a) & (b)).

Figure 8 shows response curves of the four important variables of the model. Each graph shows how the Maxent logistic prediction changes with changing environmental variables while all other variables are held at a constant value. Looking at the response curves, we notice that the gorse model responded highly to the annual precipitation (bio12) and aridity index (res_ai_yr) variables and predicted probability of suitable conditions increases continuously with increasing long range of values. For annual mean temperature (bio1), prediction decreases with increasing values. For mean temperature of warmest quarter (bio10), prediction increases at low values and becomes static at an early stage.

Maxent also generates a second set of response curves considering only the corresponding variable and ignoring all other variables for better interpretation of variable response (Fig. 9). In this second set of response curves, annual precipitation (bio12) and aridity index (res_ai_yr) behaved similarly as in the first set of response curves. The response curve of annual mean temperature (bio1) indicates that predicted suitability decreases with increasing annual mean temperature but the trend is relatively higher in the second set. Mean temperature of warmest quarter (bio 10) shows a different pattern in the second set. In this curve the predicted suitability increases rapidly and starts declining immediately to the zero level (no prediction). Similar patterns of response in these variables when considered as an ensemble or alone (Fig. 8 and Fig. 9) signify that these variables are not closely correlated.

Figure 10 shows the Maxent model (cumulative output) projected to whole Australia. In this figure, areas in Victoria, Tasmania and New South Whales are shown in a warmer color as areas with a high predicted occurrence of gorse. The predicted suitable conditions for gorse are very low in the other areas of Australia. Predicted areas of *U. europaeus* in Australia at 10 percentile training presence are given in Figure 11. The gorse location data were overlaid on this predicted area and points fell within the predicted area.

Maxent projection to Sri Lanka using Maxent software

Figure 12 shows the Maxent model (cumulative output) projected to the Indian sub-continent. In this figure, the central mountain areas of Sri Lanka are shown in a warmer color as areas with a high predicted occurrence of gorse, and the south eastern wet zone and a few patches of South India are shown in less warm colors with low probabilities of predicted occurrences. The predicted suitable conditions for gorse are very low in the other areas with cooler (blue) colours. Predicted areas of *U. europaeus* in the Indian sub-continent at a 12.295 cumulative threshold derived from the 10 percentile training presence are given in Figure 13. The gorse location data collected from Sri Lanka during our field work were overlaid on this predicted area and all points fell within the predicted area. Figure 14 shows an array plot of the raster stack of seven predictor variables used for the *U. europaeus* model in the Indian sub-continent. All seven predictor variables have distributions that are well correlated with the predicted area map we received for Sri Lanka from the Maxent projection.

Multiple SDM model comparison with R for South Australia

Figure 13 shows predictions of the distribution of gorse in southern South Australia under four modelling algorithms; GLM, Bioclim, Domain and Maxent, individually run in the ‘dismo’ package in R. The four models performed slightly differently, with the highest model AUC of 0.9632 achieved with the Maxent model, suggesting that this model best fit the data. The Maxent prediction is relatively more conservative in comparison with the other models, GLM, Bioclim and Domain suggesting that the latter three models may overestimate the suitable climate space. Table 5 provides summary statistics for the GLM model that contains individual test parameters for environmental variables. The statistics imply that all variables except mean temperature of the warmest quarter (bio 10) made significant contributions to the prediction of habitat suitability for gorse. Table 6 shows results of the evaluation of fitted models produced by GLM, Bioclim, Domain and Maxent. Out of the four modelling algorithms, Maxent shows highest model AUC and relatively higher model robustness.

Three models, Bioclim, Domain and Maxent predict the presence of gorse on the Yorke and Eyre peninsulas at varying levels of magnitude. The GLM model does not predict the presence of gorse in these regions.

SDM model projection to Sri Lanka using the ‘dismo’ package in R for *Ulex europaeus*

The model projection to the Indian sub-continent was again conducted with the Maxent modelling technique in the ‘dismo’ package in R. We overlaid the few localities of gorse derived from our field work in Sri Lanka on the Maxent presence-absence prediction (Fig. 14). The prediction picture we received under ‘dismo’ for the Indian sub-continent is quite similar to the prediction picture we received earlier using the stand-alone Maxent software at a 10 percentile training presence.

Analysis of values of environmental variables in South Australia and Sri Lanka

The summary output of the cell values of each environmental layer in South Australia and in Sri Lanka are given in table 7. The range of cell values of each layer in Sri Lanka was higher than the relevant value range in layers of South Australia.

DISCUSSION

Ulex europaeus is an alien invasive species in many countries in the world. Thus, prediction of the potential distribution patterns of *Ulex europaeus* using Bioclimatic modelling is an important aspect of understanding the likely impact of this noxious species in countries of its invasive range such as South Australia and Sri Lanka.

Species distribution modelling with Maxent software for *Ulex europaeus* in South Australia

Several successful studies have been done using the default settings of the Maxent program (Webber *et al.* 2011; Wilson *et al.* 2011). The auto features perform slightly better than other features for presence-only herbarium data (Syfert *et al.* 2013). Our *U. europaeus* model performed well with default settings with relatively high model AUC and model gain. Maps from SDM represent the potential distribution of the species based on the postulated links between species data and environmental variables, and since invasive species tend to expand their habitat to acquire all climatically suitable habitats, such models are likely to be useful predictors of the ultimate range of invasive species (Wilson *et al* 2011). Gorse was established both in South Australia and Sri Lanka more than 100 years ago. Based on our predicted presence-absence map at our selected threshold, gorse was predicted to be widely distributed in the Mount Lofty Ranges and Kangaroo Island areas in South Australia. We found that our herbarium occurrence points were distributed in most of the suitable areas of the presence-absence map, showing that this species has already occupied most of its favourable climatic gradient in South Australia. Having confidence that SDM models capture key determinants of the fundamental niche is important to properly apply them to understand species invasions (Webber *et al.* 2011). The majority of our species environmental data obtained from the Worldclim database are averaged over a long time period (1950 to 2000), therefore we believe that data are likely to represent the relevant environmental variability experienced by gorse and so provide a realistic prediction.

Geographical sampling bias is a critical issue in SDM studies based on open access data portals (Syfert *et al.* 2013). In this study the occurrence data are spread across the predicted suitable locations (Fig.4) indicating that environment corresponding to the presence points may be representative of the overall climatic niche of *U. europaeus* (Scheldeman and Van Zonneveld 2010). The high rate of false absences results in bad performance models (Lobo *et al.* 2010). Localities where the study species has not been recorded may not be directly causing significant differences to the model prediction if the study area is large enough to capture the environmental variability of the study species and the occurrence points are distributed in most of the suitable areas of the presence-absence map. SDM predictions can over-estimate ranges if they omit factors that limit the spread of species such as natural barriers, soil type, predators and competition by closely related species (Xavier and Van Zonneveld 2010). However, gorse can grow on a wide range of soil types including sands, clays and clay loams other than soils rich in calcium (Centre for Environmental Management University of Ballarat 1999). Honey bees (*Apis mellifera* L.), the primary pollinators of gorse (Bowman *et al.* 2008) are widespread in every continent except Antarctica (Goulson 2003). Therefore, neither of these factors would likely contribute to overestimating the range of this species. The threshold value which is set for model prediction is an arbitrary value (Liu *et al.* 2005) hence the prediction of potential area could vary with the selected threshold. For example our *Ulex europaeus* model prediction very much increased when we used the “minimum training presence” criterion in Maxent where the cumulative threshold is 0.753.

Analysis of our jackknife tests revealed that annual rainfall was a critical factor in affecting the distribution of gorse in South Australia. The aridity index, which is an indicator for the degree of dryness and calculated by the ratio of annual potential evaporation to precipitation (Arora 2002) also significantly affected the model prediction. Therefore, suitable conditions for gorse will depend on the level of dryness caused by the evaporation or more combined effect associated with those variables. annual mean temperature (bio1) and mean temperature of warmest quarter (bio10) also make considerable contributions to the model. Isothermality, which is a measure derived from temperature values (mean diurnal range /temperature annual range * 100), weakly influences the distribution of gorse in this climate regime.

The prediction we received for Australia was quite realistic because occurrence points were overlaid on the prediction area (Fig. 11). This implies that the Maxent fitted model for gorse in South Australia has captured the considerable environmental variable gradient of the species.

Maxent projection to Sri Lanka using Maxent software

From our field study, gorse is restricted to a small patch in the central mountain mass in Sri Lanka. Therefore, we could collect only a few occurrence points during our field survey. The points we collected were quite close to each other and therefore, these species data are not quite enough on their own to directly derive a Maxent model for Sri Lanka. Nevertheless, we were able to project a Maxent model derived from South Australian records to successfully predict the occurrence of gorse plants in Sri Lanka, even though the available areas for gorse in South Australia and Sri Lanka are climatically distinct. Projections are needed when modelling species distributions under changing climate conditions (Phillips 2010). The prediction we received for Sri Lanka was quite small and realistic because our few occurrence points were overlaid on the prediction area (Fig. 11). This also implies that the Maxent fitted model for gorse in South Australia has captured the considerable environmental gradient of the species to make a prediction in a climatically distinct area.

In Sri Lanka, gorse is restricted to a few very small patches in central highland area. However, the prediction we received (Fig. 11) is larger than the actual distribution we observed. Therefore, we believe that gorse has the potential to spread further in Sri Lanka and hence that management should consider relevant precautionary actions to control the spread of this species in central highlands in Sri Lanka. During our field visits we observed isolated gorse plants which were flowering and fruiting in several places in the central highlands, indicating the climatic suitability for the gorse distribution in these areas.

Selection of suitable environmental parameters is an important and challenging step of the modelling process. Our first attempt to transfer the gorse model fit with Worldclim monthly data was not successful. In this analysis the prediction we received for South Australia was similar as with the Bioclim variables we used later, but the algorithm reversed the prediction areas when we projected the model to Sri Lanka. In comparison to the monthly climatic parameters in the Worldclim database (monthly maximum and minimum temperature and precipitation), the derived Bioclim variables, such as "annual precipitation” or “mean temperature of warmest quarter” do not specify a particular time of the year or month. This is extremely important when projecting a model to a different hemisphere where the climatic conditions in a particular period may be completely reversed.

Webber *et al*. (2011) point out that projection of correlative models especially to novel climates should be done carefully because they can make biologically unrealistic projections when the response functions of certain parameters exceed model behaviour. We investigated the values of each variable applicable to these two countries which indicated the ranges of values are quite different. Therefore, same variables may perform in a different manner in climatically distinct areas.

Multiple SDM model comparison with R

Spatial predictions may vary significantly among various models due to the differences in modelling algorithms and assumptions used (Syphard and Franklin 2009). However, our study found quite similar and realistic projected range limits for *Ulex europaeus* in South Australia using four different modelling techniques, GLM, Bioclim, Domain and Maxent. The overall mean of AUC values across all models we received was 0.95 and all models individually exceeded a model AUC of 0.93, indicating that all models provided a good fit to the data.

In multiple model comparisons using the ‘dismo’ package in R, the GLM, Bioclim and Domain models predicted comparatively greater predicted areas as suitable for gorse distribution than did the Maxent model. However, model evaluation shows Maxent as the most robust model with relatively better discrimination ability.

AUC is considered as an important metric to quantify model performance (Syphard and Franklin 2009). In our exercise we received the highest AUC value with Maxent where the predicted area map is smaller compared with other three models. The lowest model performance out of the above four models was observed in Bioclim where the prediction map extent is highest. The other two models GLM and Domain have moderate levels of AUCs. The AUC represents a probability for observations where prediction for presence observations is higher than the prediction for absence observation (Syphard and Franklin 2009). However, we get higher AUC in Maxent where we have relatively less prediction. This may be due to some other factors, such as model prevalence or map correlation, that vary with the modelling method used.

Conclusion

The distribution of gorse (*Ulex europaeus)* species in South Australia has been modelled using 126 presence-only location data as a function of seven climate parameters. The discrimination capacity of this distributional model developed using presence-only herbarium data of South Australia received from the state herbarium of South Australia was determined by calculating the area under the receiver operating characteristic curve (AUC) criterion. The resulting gorse model was found to have good discrimination ability of presence and absence, with very high AUC value of 0.974.

The Jackknife procedure was employed to identify the variable contribution for gorse model outputs, and response curves were used to predict changes with changing environmental variables. Based on the jackknife test analyses we found that the combined effect of one or more variables could have a completely different impact on the model output than any of the original variables on their own. Our work also demonstrates the need for a careful approach when selecting environmental variables for projecting correlative models to climatically distinct area and the utility of relativized, rather than absolute, measures of climatic conditions.

Our projection of a Maxent model trained with environmental variables of South Australia to relevant layers of Sri Lanka brings valuable insight for applications in changing climate conditions. The prediction we received for Sri Lanka encompassed our known occurrence localities which are restricted to a few small patches but is larger than the actual area of gorse distribution, suggesting a capacity for gorse to expand its range in this region. These findings are important not only to predict and manage invasive alien gorse in South Australia and Sri Lanka but also in other countries of the invasive range.

ACKNOWLEDGEMENTS

We would like to thank the Department of Environment and Natural Resources, Government of South Australia and Department of Wildlife conservation, Sri Lanka for permitting us to undertake scientific research within the State’s system of conservation reserves. We would like to acknowledge the State Herbarium of South Australia for providing *Ulex europaeus* herbarium records for the study.

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Table 1 Locations of Sri Lankan gorse (*Ulex europaeus*)

District / Region	**Locality**	**Chosen Lat**	**Ch Lat dir**	**Chosen Lon**	**Ch Lon dir**	**collection date**	**Frequency Notes**	**Habitat Notes**
Nuwara Eliya	Horton Plains national park - check point	6°48’8”	N	80°48’27”	E	22-Nov-12	Common	roadside thickets.
Nuwara Eliya	27th km post from Nuwra Eliya to Horton plains road	6°48’13”	N	80°48’24”	E	23-Nov-12	Common	roadside thickets.
Nuwara Eliya	Horton Plains National park	6°50’34”	N	80°48’54”	E	29-Nov-12	Common	
Nuwara Eliya	Ambewela farm, Nuwara Eliya	6°53’4”	N	80°48’19”	E	21-Dec-12	Localized patch	
Nuwara Eliya	Nuwara Eliya Racecourse	6°57’40”	N	80°46’19”	E	20-Jan-13	Common	around the boundary of the racecourse
Nuwara Eliya	Horton Plains	6°47’58”	N	80°48’6”	E	21-Nov-12	Common	site 1-trail to Kirigalpota
Nuwara Eliya	Horton Plains	6°47’58”	N	80°48’7”	E	19-Jan-13	Common	site 1-trail to Kirigalpota

Table 2 Selected parameters and their codes

Parameter	**Code**
annual mean temperature	bio1
isothermality	bio2/bio7 * 100 (bio3)
max temperature of warmest month	bio5
mean temperature of warmest quarter	bio10
annual precipitation	bio12
precipitation seasonality (coefficient of variation)	bio15
yearly average aridity index	res_ai_yr

Table 3 Some common thresholds and corresponding omission rates resulted by the *Ulex europaeus* model in South Australia

Cumulative threshold	**Logistic threshold**	**Description**	**Fractional predicted area**	**Training omission rate**	**Test omission rate**	**P-value**
1.000	0.004	Fixed cumulative value 1	0.381	0.013	0.000	3.361E-11
5.000	0.027	Fixed cumulative value 5	0.152	0.013	0.000	3.454E-21
10.000	0.067	Fixed cumulative value 10	0.084	0.080	0.080	4.708E-23
0.753	0.003	Minimum training presence	0.426	0.000	0.000	5.496E-10
12.295	0.098	10 percentile training presence	0.068	0.093	0.080	3.226E-25
10.490	0.073	Equal training sensitivity and specificity	0.080	0.080	0.080	1.517E-23
7.072	0.045	Maximum training sensitivity plus specificity	0.116	0.027	0.000	3.961E-24
10.490	0.073	Equal test sensitivity and specificity	0.080	0.080	0.080	1.517E-23
7.736	0.050	Maximum test sensitivity plus specificity	0.107	0.053	0.000	5.843E-25
4.668	0.025	Balance training omission, predicted area and threshold value	0.160	0.013	0.000	1.254E-20
13.004	0.107	Equate entropy of thresholded and original distributions	0.064	0.107	0.080	8.083E-26

Table 4 Contribution of environmental variables for *Ulex europaeus* model

Parameter	Percent contribution	Permutation importance
annual precipitation	60.1	8.5
yearly average aridity index	28.9	32.4
precipitation seasonality (coefficient of variation)	5.9	20.8
mean temperature of warmest quarter	2.3	5.9
Isothermality	1.8	18.8
max temperature of warmest month	0.8	9.1
annual mean temperature	0.2	4.5

Table 5 Summary statistics for the GLM model object

Coefficients:				
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	-1.369e+00	1.091e-01	-12.544	< 2e-16 ***
annual mean temperature	3.452e-03	5.710e-04	6.045	1.57e-09 ***
mean temperature of warmest quarter	-1.074e-03	8.336e-04	-1.288	0.197799
annual precipitation	6.457e-04	5.513e-05	11.712	< 2e-16 ***
precipitation seasonality (coefficient of variation)	-2.616e-03	1.636e-04	-15.993	< 2e-16 ***
isothermality	5.558e-03	1.446e-03	3.843	0.000123 ***
max temperature of warmest month	1.893e-03	3.282e-04	5.767	8.36e-09 ***
yearly average aridity index	2.048e-05	6.444e-06	3.178	0.001487 **

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.00896686)

Null deviance: 89.909 on 7590 degrees of freedom
Residual deviance: 67.996 on 7583 degrees of freedom
(3 observations deleted due to missingness)
AIC: -14233

Number of Fisher Scoring iterations: 2

Table 6 Results of the evaluation of models, GLM, Bioclim, Domain and Maxent

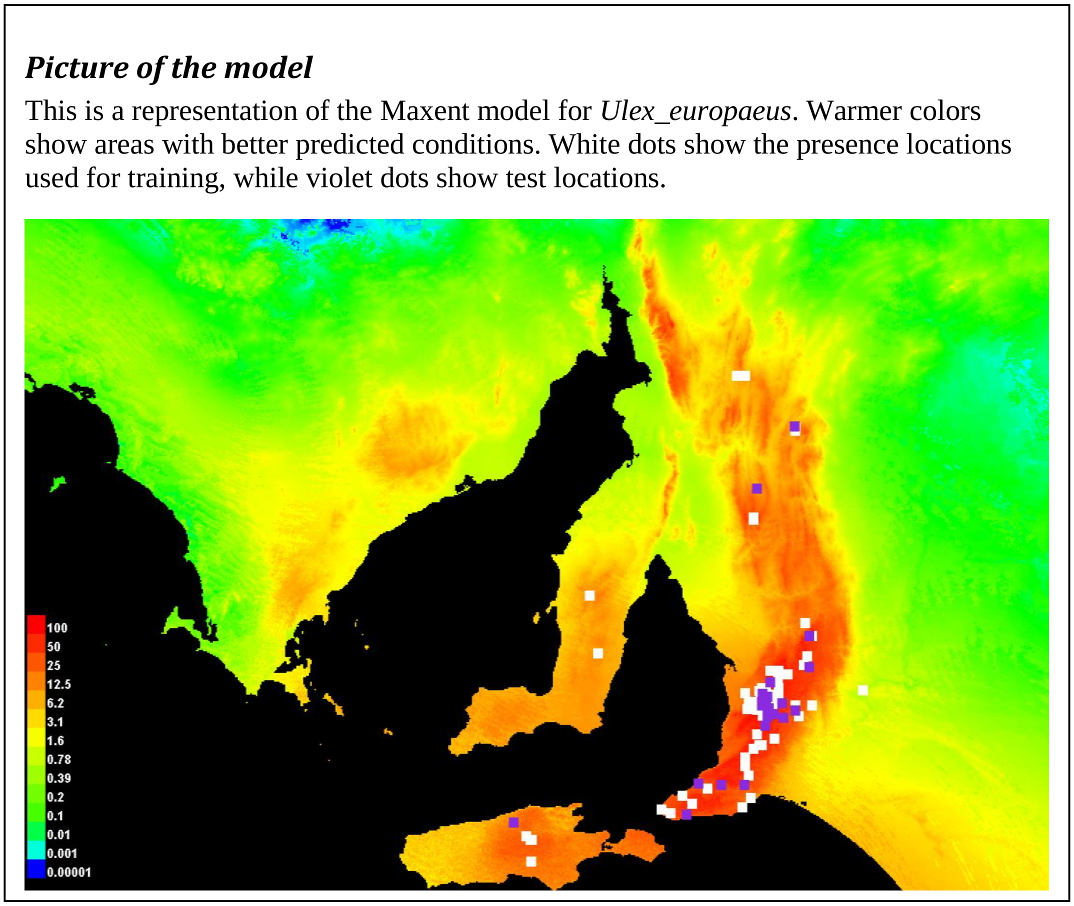
GLM	**Bioclim**	**Domain**	**Maxent**
n presences : 30 n absences : 2500 AUC : 0.9508133 cor : 0.2707805 max TPR+TNR at : -4.834903	n presences : 30 n absences : 2500 AUC : 0.93862 cor : 0.4525172 max TPR+TNR at : 0.00681209	n presences : 30 n absences : 2500 AUC : 0.9583267 cor : 0.2627793 max TPR+TNR at : 0.4253808	n presences : 30 n absences : 2500 AUC : 0.9631733 cor : 0.4854979 max TPR+TNR at : 0.03133848

Table 7 Summary of cell values of each environmental layers in South Australia (SA) and Sri Lanka (SL)

	Min	**1st Q**	**Median**	**Mean**	**3rd Q**	**Max**	**NA's**
annual mean temperature (SA)[1]	124.0	158.0	164.0	162.9	169.0	188.0	122275.0
annual mean temperature (SL)[1]	122.0	256.0	272.0	265.4	282.0	293.0	721061.0
isothermality (SA)[1]	45.0	49.0	50.0	50.4	52.0	54.0	122275.0
isothermality (SL)[1]	49.0	58.0	61.0	61.4	64.0	81.0	721061.0
max temperature of warmest month (SA)[1]	221	289	305	300	317	335	122275
max temperature of warmest month (SL)[1]	190	325.0	340.0	339.5	362.0	386.0	721061.0
mean temperature of warmest quarter (SA)[1]	173.0	209.0	220.0	218.6	229.0	253.0	122275.0
mean temperature of warmest quarter(SL)[1]	138.0	275.0	289.0	285.7	306.0	321.0	721061.0
annual precipitation (SA)[2]	9.00	22.00	34.00	33.91	44.00	65.00	122275.00
annual precipitation (SL)[2]	24.0	71.0	78.0	79.8	88.0	147.0	721061.0
precipitation seasonality (SA)[2]	9.00	22.00	34.00	33.91	44.00	65.00	122275.00
precipitation seasonality (SL)[2]	24.0	71.0	78.0	79.8	88.0	147.0	721061.0
yearly average aridity index (SA)[2]	1326	1855	2477	2784	3283	9806	122275
yearly average aridity index (SL)[2]	2773	4794	6910	9904	12840	48320	721061

1 = Temperature data is in units of °C * 10

2 = Precipitation data in units of mm



Picture of the model

This is a representation of the Maxent model for *Ulex_europaeus*. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations.

Fig. 1 Picture of the Maxent model (cumulative output) for *Ulex europaeus* in South Australia

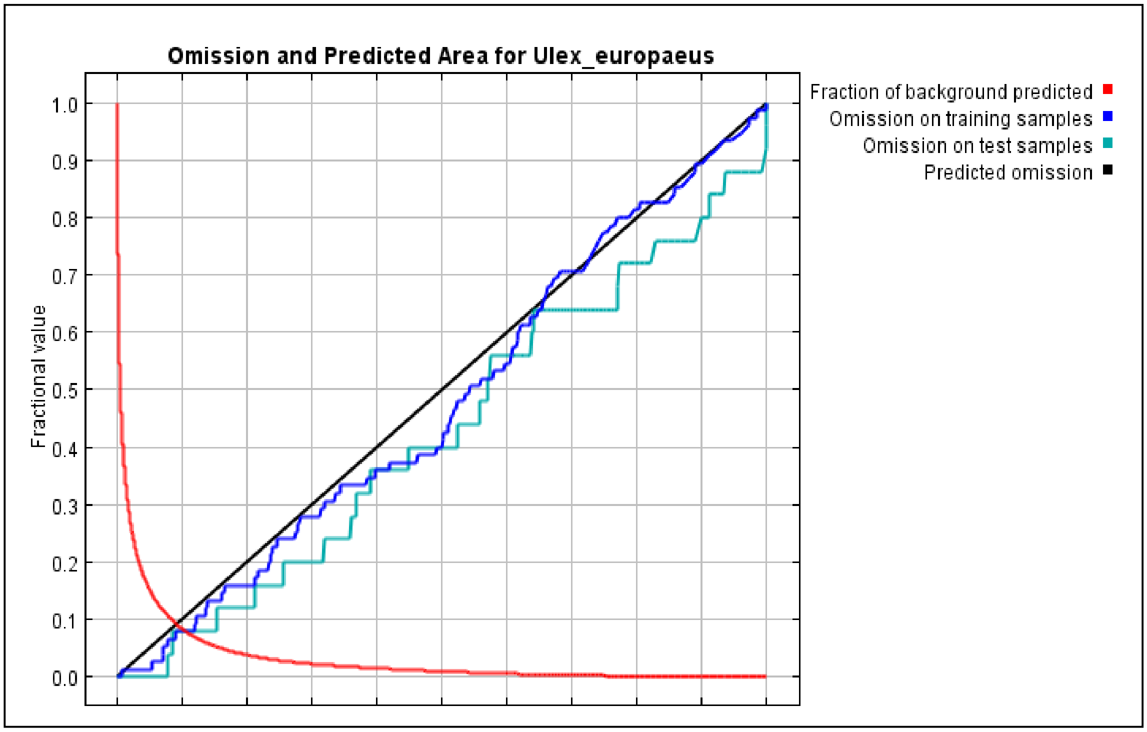


Fig. 2 Omission and predicted area for *Ulex europaeus*

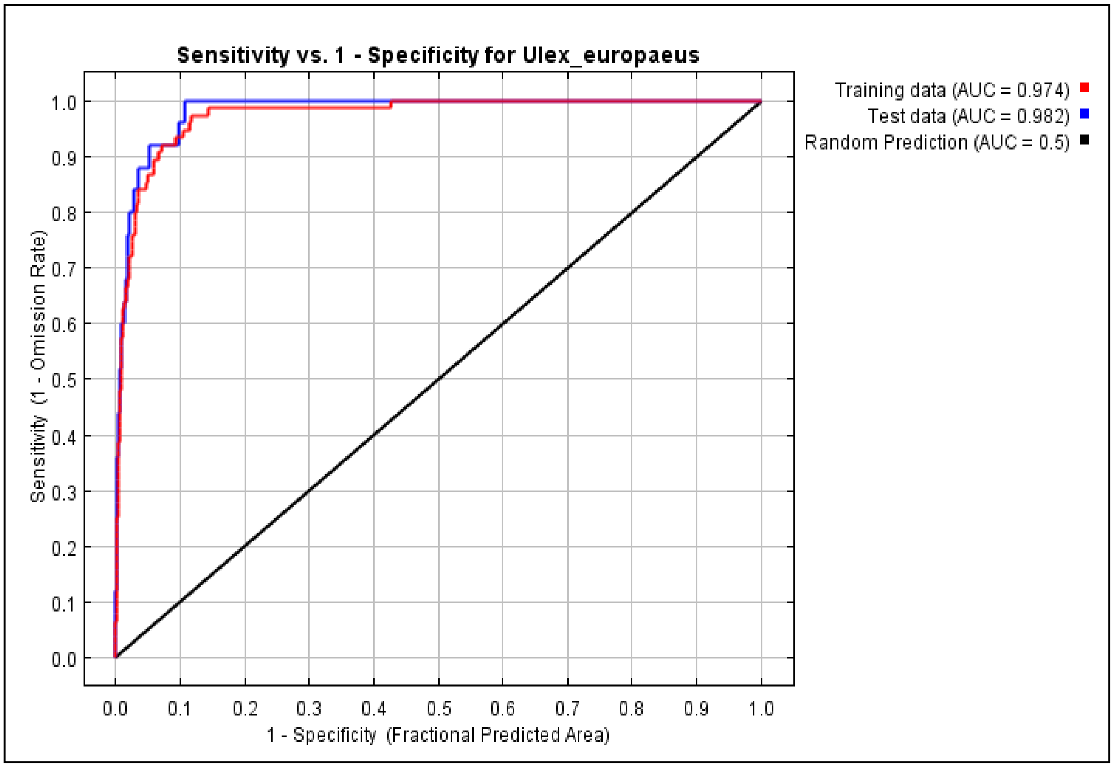


Fig. 3 Sensitivity Vs 1-specificity curve for *Ulex europaeus*

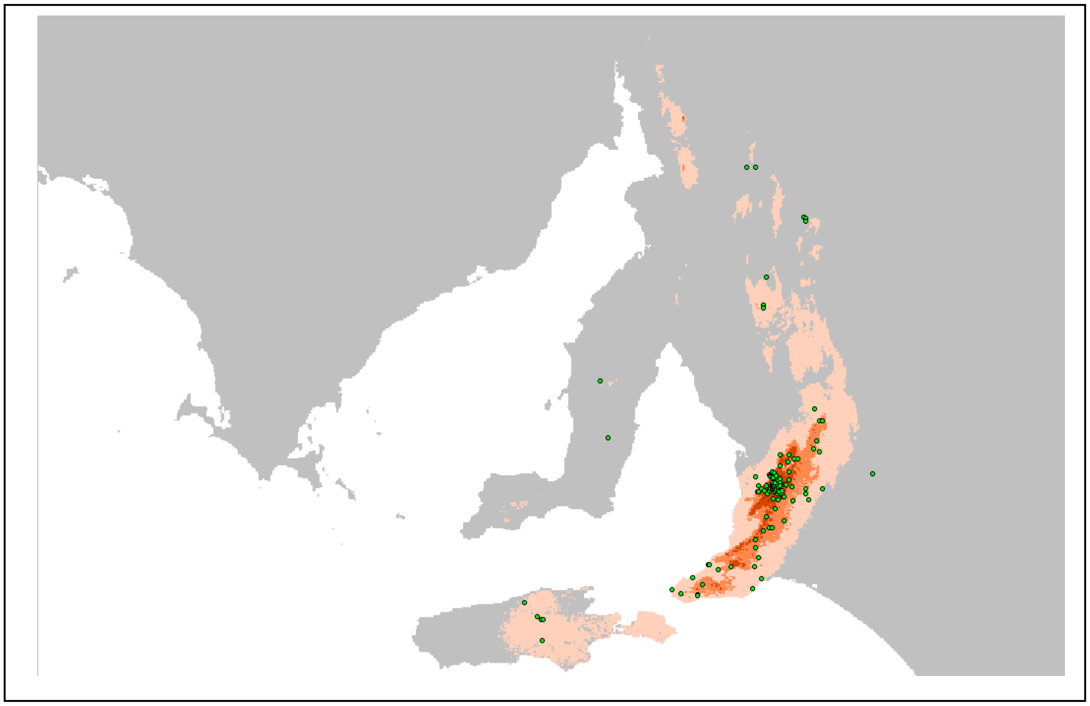


Fig. 4 Predicted areas of *Ulex europaeus* in South Australia at 12.295 cumulative threshold (10 percentile training presence). Green dots indicate occurrence records of *U. europaeus* in South Australia.

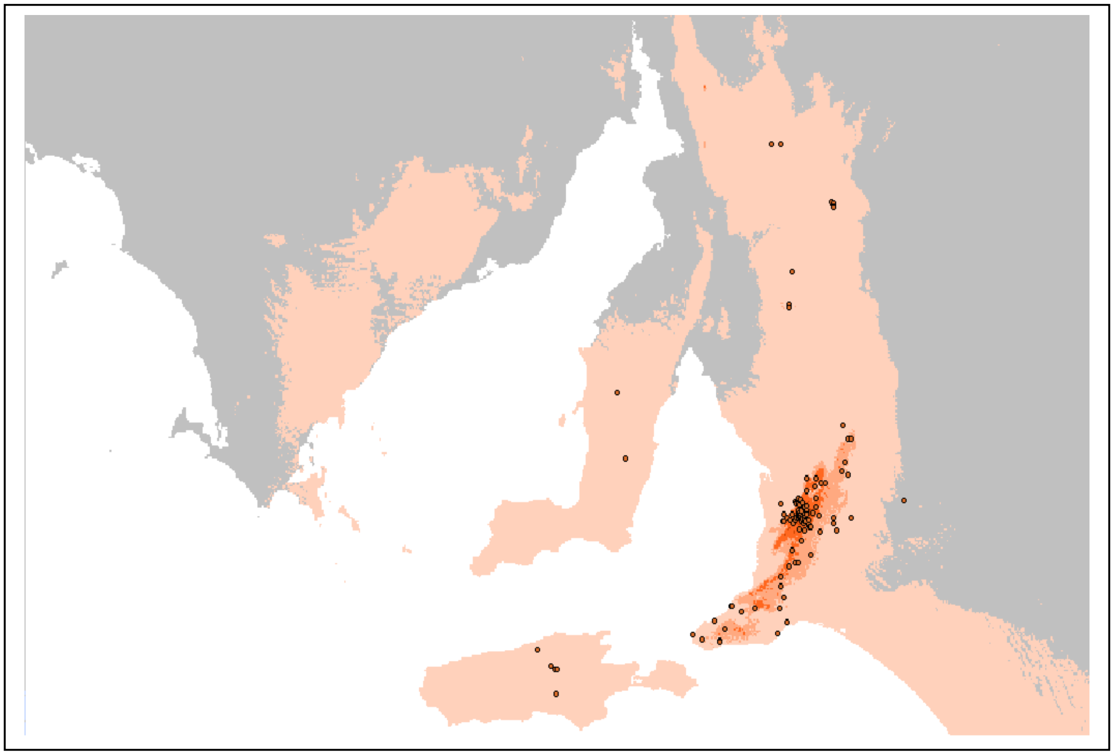


Fig. 5 Predicted areas of *Ulex europaeus* in South Australia at a 0.753 cumulative threshold (minimum training presence). Red dots indicate occurrence records of *U. europaeus* in South Australia.

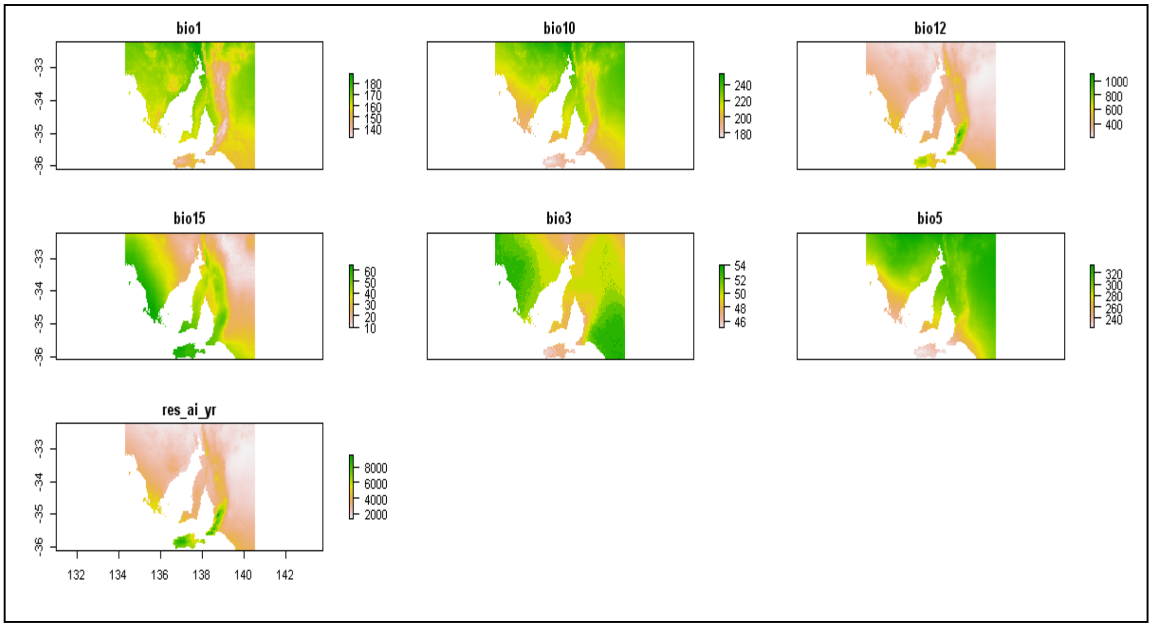


Fig. 6 Raster stack of seven predictor variables used for the *Ulex europaeus* model in South Australia

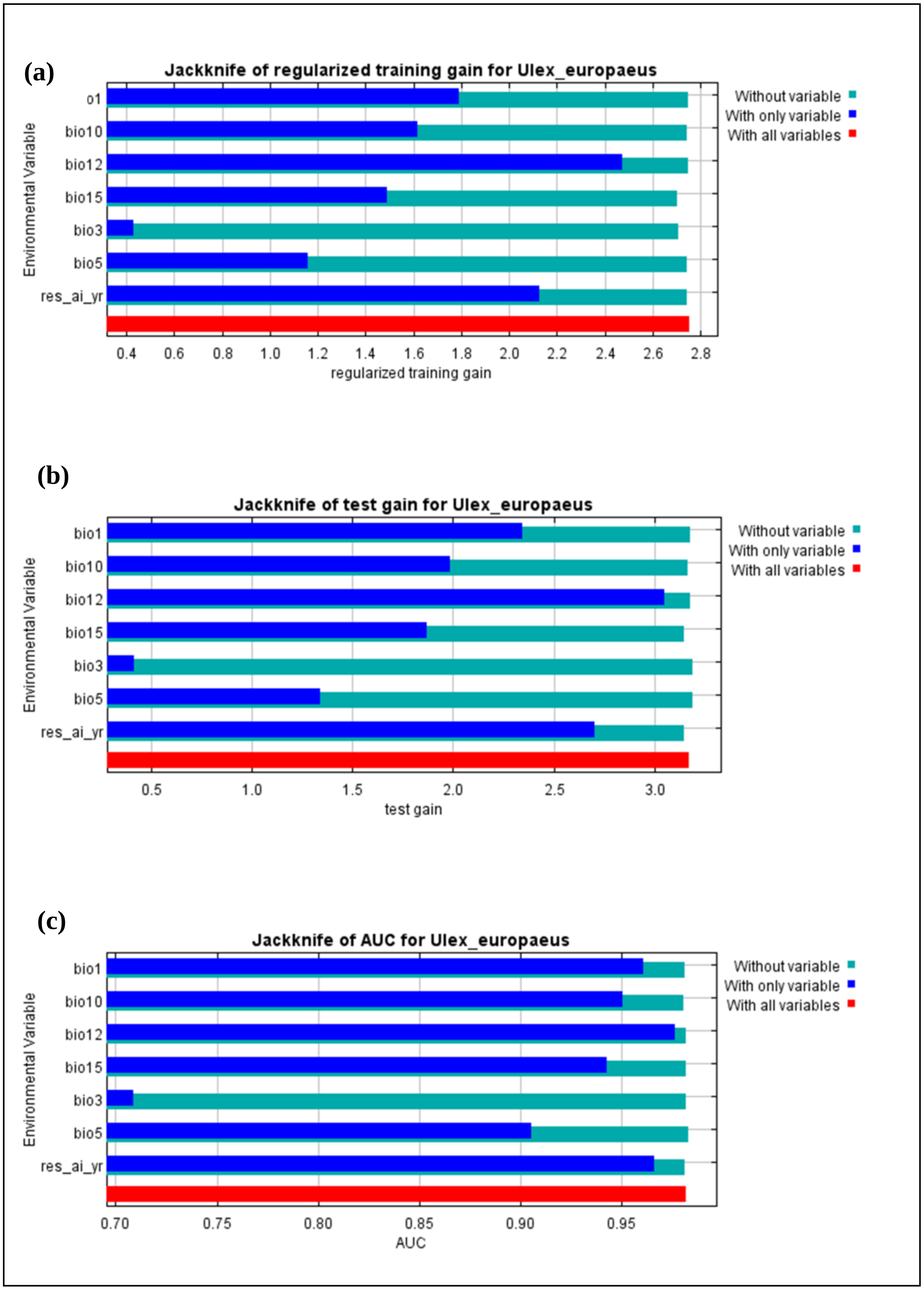


Fig. 7 Results of Jackknife test of variable importance in the regularized training gain (a), test gain (b) and AUC (c) for *Ulex europaeus* model

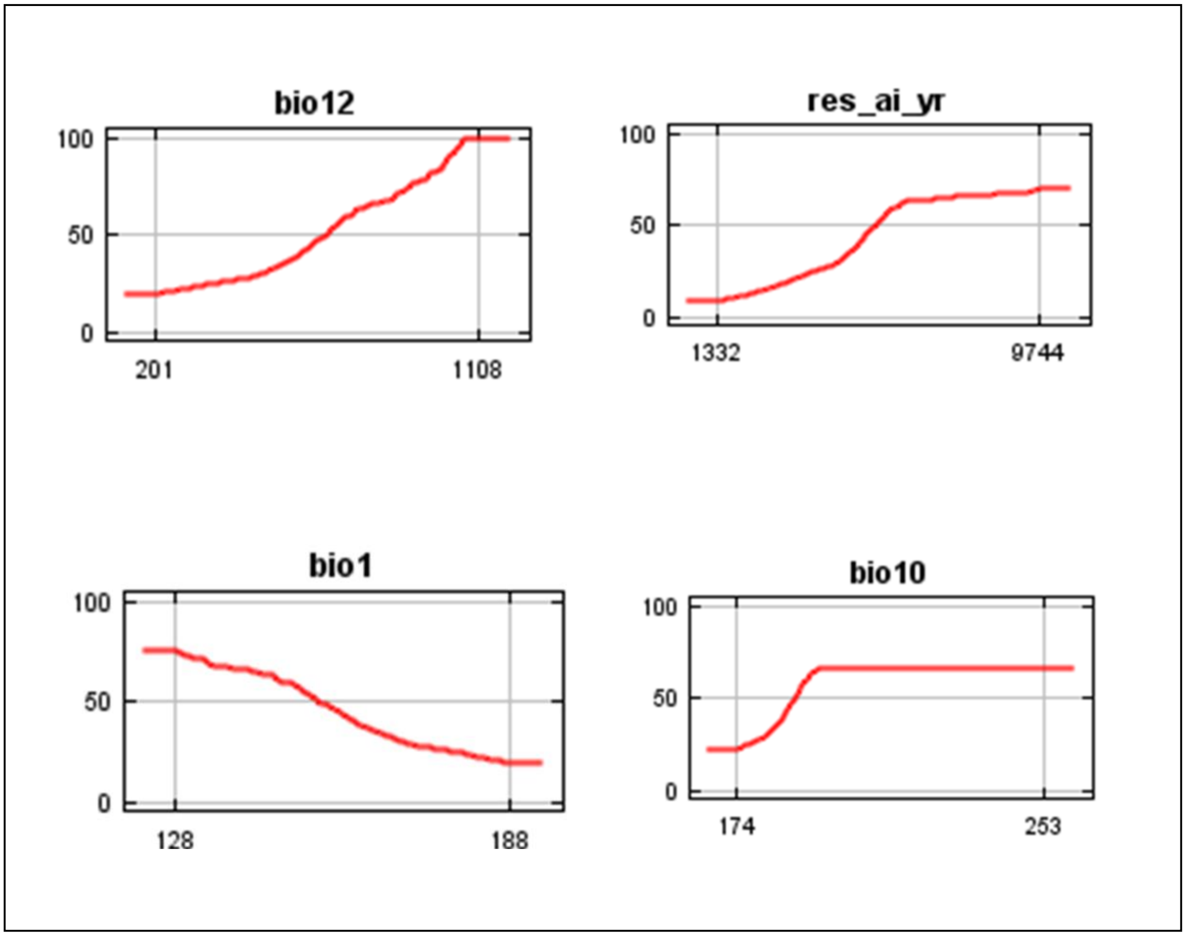


Fig. 8 Response curves of the four predictor variables (that most affected on *Ulex europaeus* model) showing how each variable affects Maxent prediction

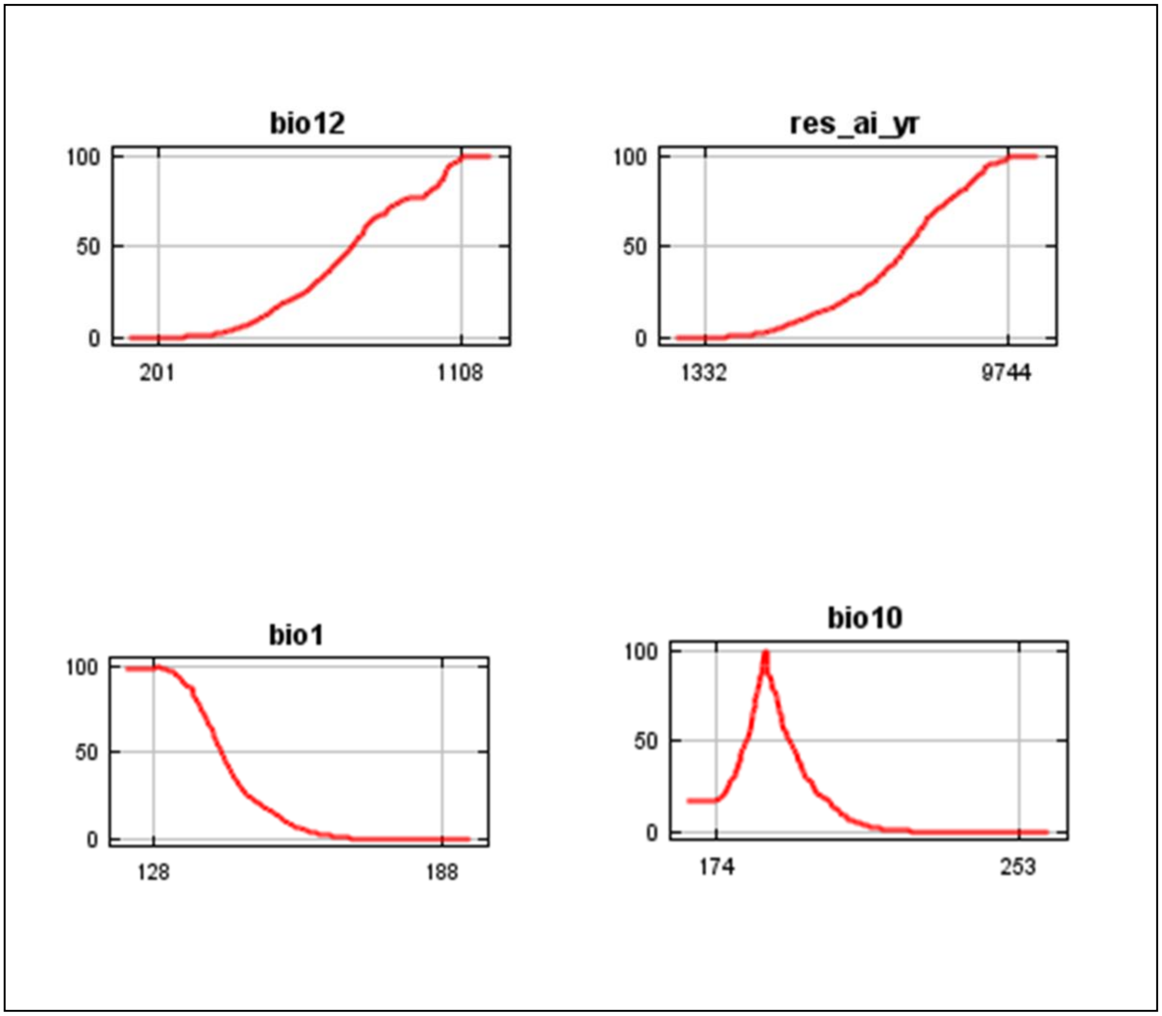


Fig. 9 Response curves considering only the corresponding variable of the above four variables.

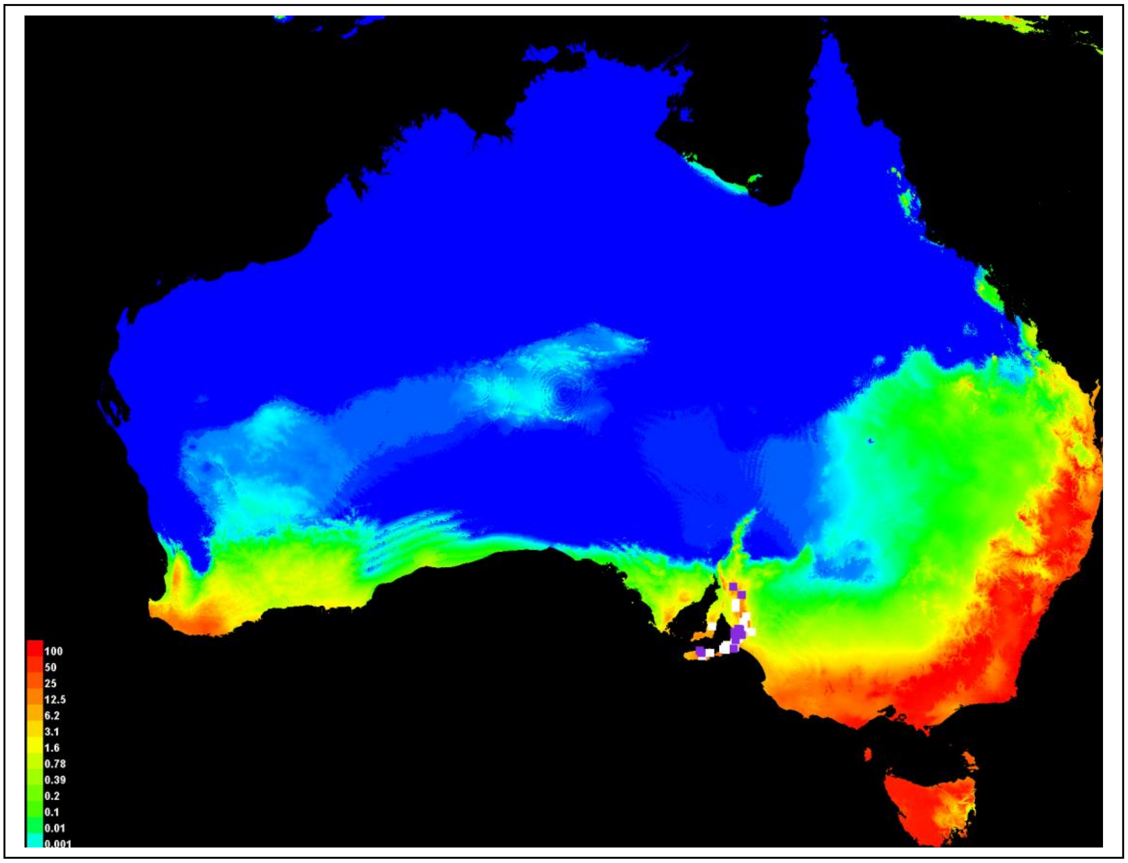


Fig. 10 Picture of the Maxent model projection (cumulative output) for *Ulex europaeus* in Australia.

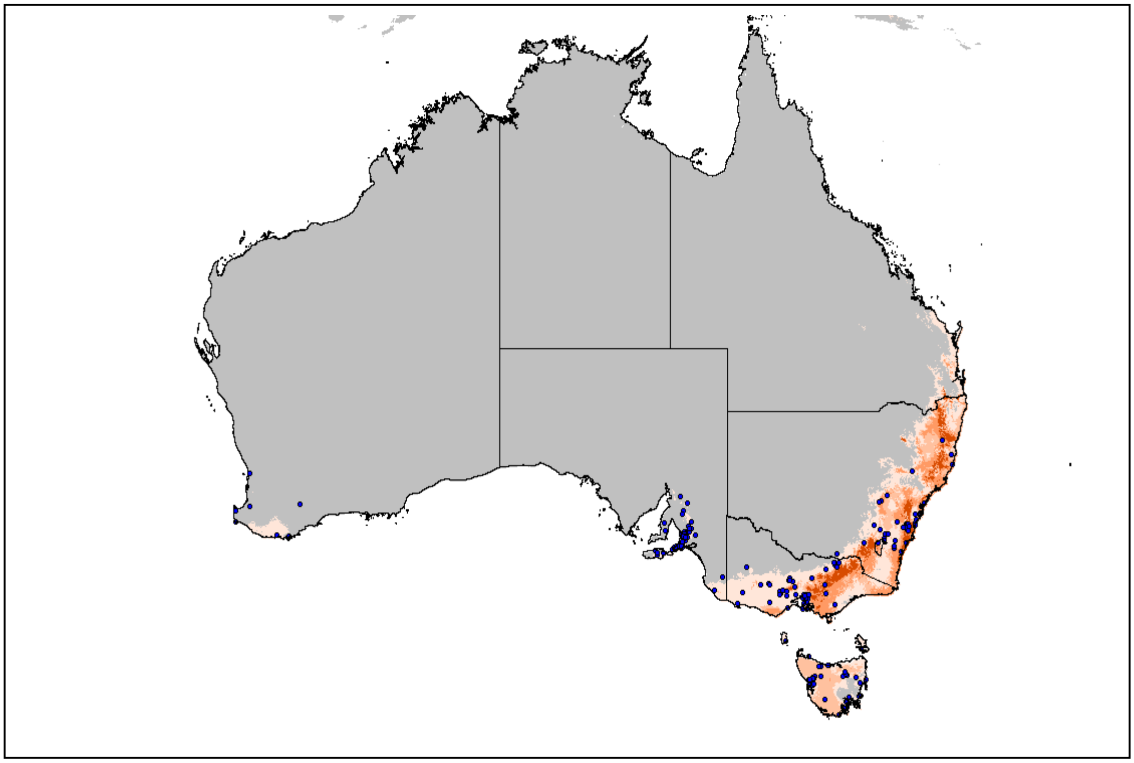


Fig. 11 Predicted areas of *Ulex europaeus* in Australia at 10 percentile training presence. Blue dots indicate occurrence records of *U. europaeus* in Australia

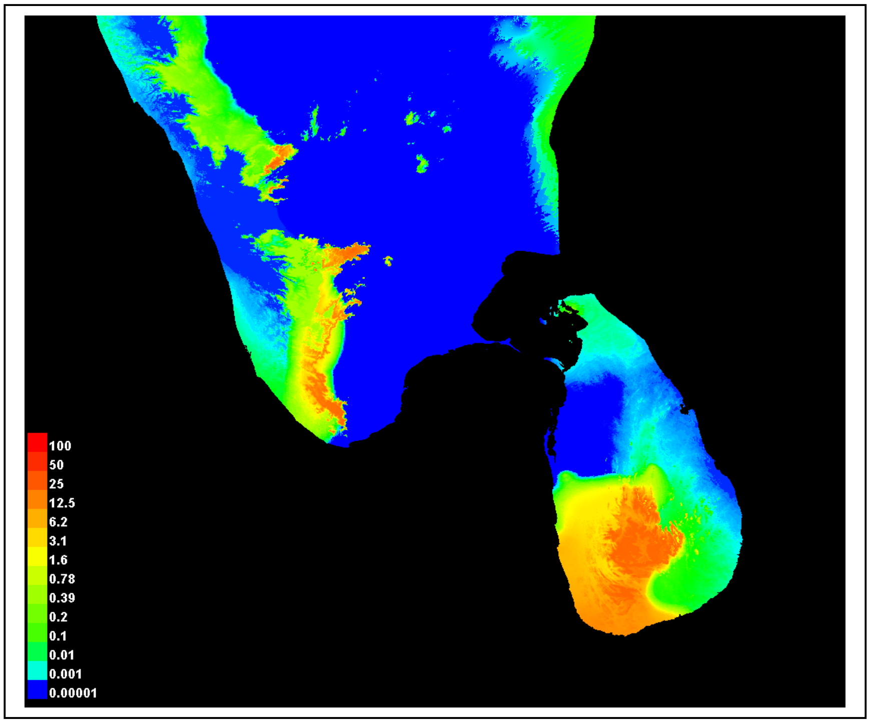


Fig. 12 Picture of the Maxent model projection (cumulative output) for *Ulex europaeus* in the Indian sub-continent

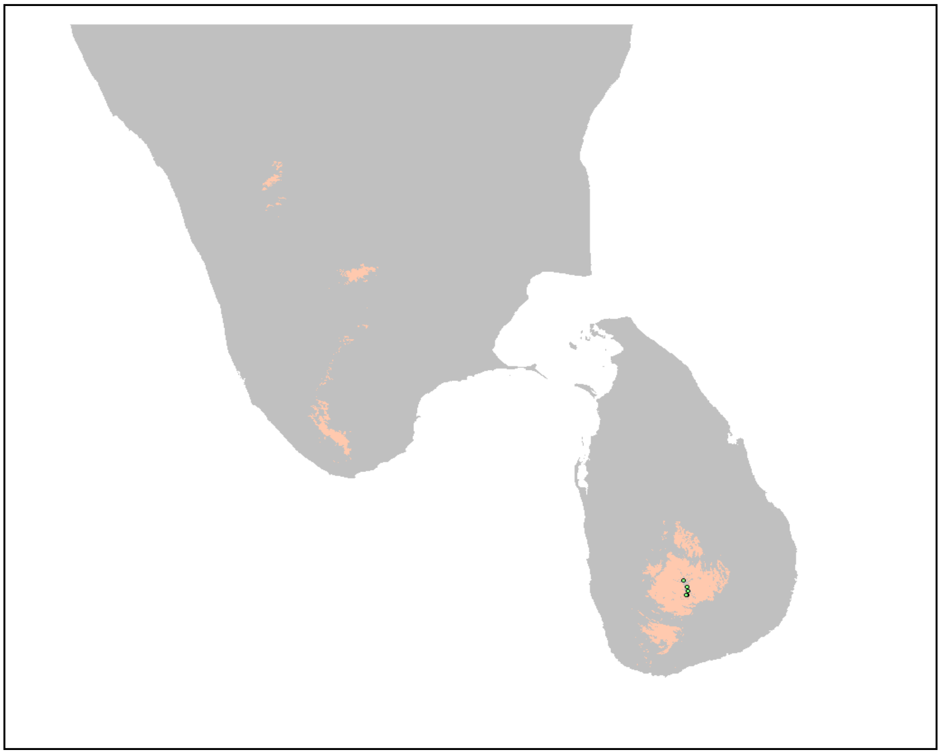


Fig. 13 Predicted areas of *Ulex europaeus* in the Indian sub-continent at a 12.295 cumulative threshold (10 percentile training presence). Green dots indicate occurrence records of *U. europaeus* in Sri Lanka.

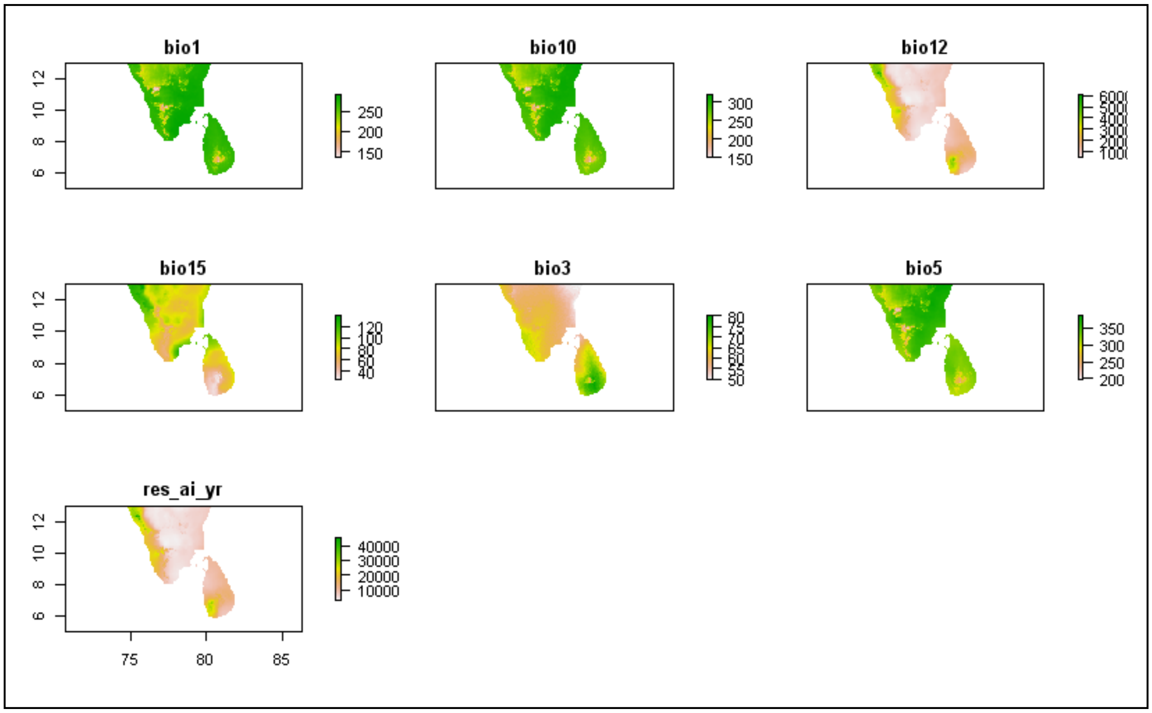
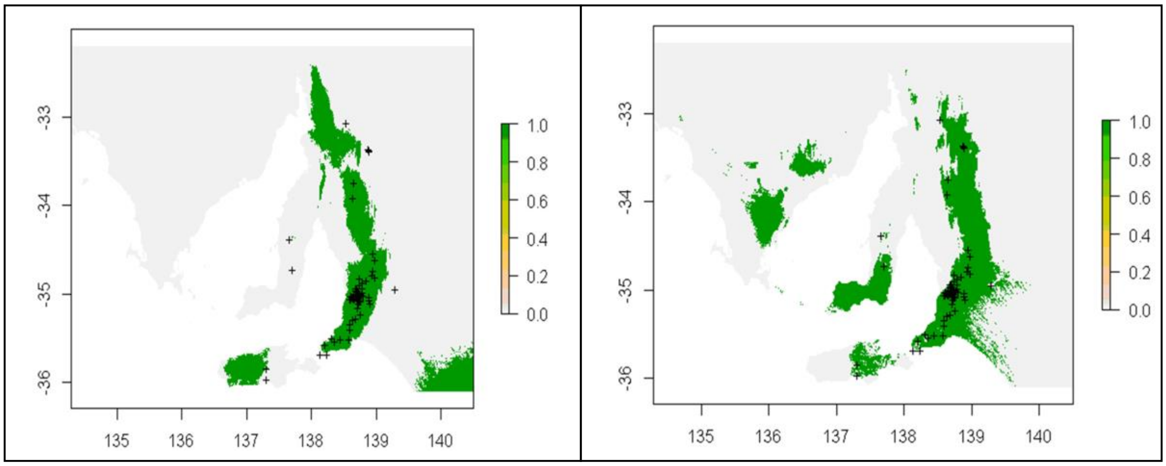
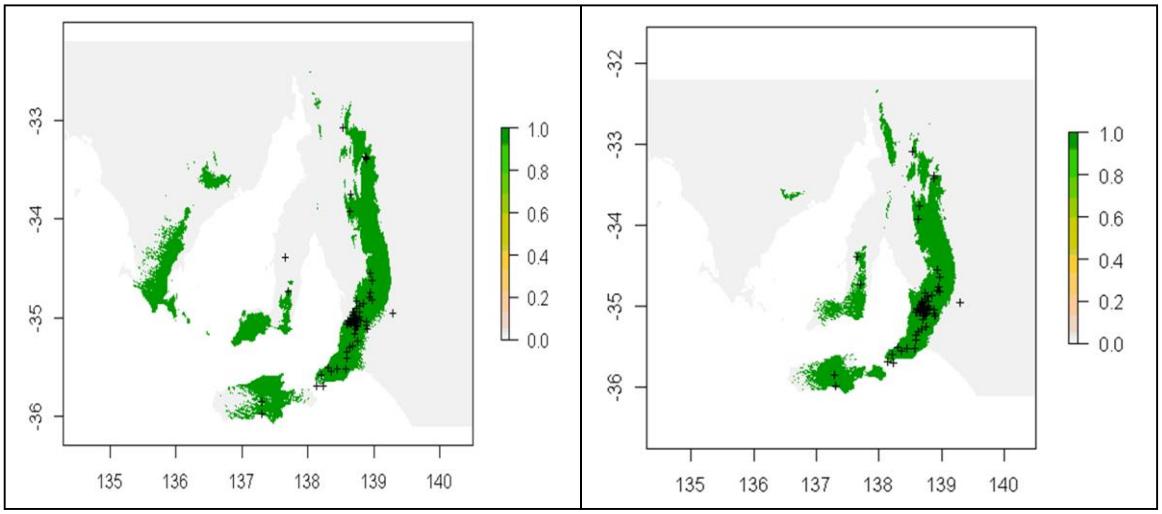


Fig. 14 Raster stack of seven predictor variables used for the *Ulex europaeus* model projection to the Indian sub-continent



GLM predicted range **Bioclim predicted range**



Domain predicted range **Maxent predicted range**

Fig. 15 Model projections for the potential distribution of *Ulex europaeus* using four modeling techniques in the 'dismo' package in R for South Australia. Small crosses indicate occurrence records of *U. europaeus* in South Australia.

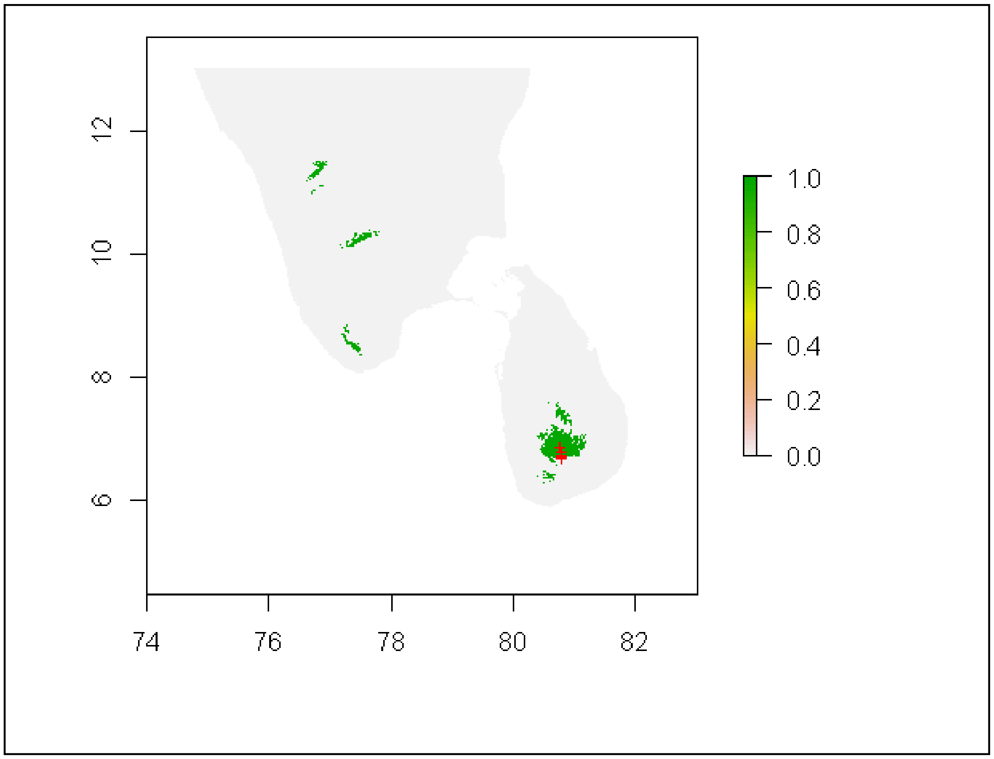


Fig. 16 Maxent model projection (run in the ‘dismo’ package in R) for *Ulex europaeus* in the Indian sub-continent with overlaid *U. europaeus* occurrences. Red crosses indicate occurrence records of *U. europaeus* in Sri Lanka.

Chapter 4

GENERAL DISCUSSION

Comparative study of the reproductive biology of gorse (*Ulex europaeus*) in the Mount Lofty Ranges of South Australia and central highlands in Sri Lanka

The reproductive biology of gorse is important to understand, since gorse is a notorious invader in several countries in the world and information on the species' reproductive biology, especially flowering and fruiting phenology, is much needed and is directly relevant to its spread and control. For example, the introduction of new biological control agents requires such information since a control agent's life-cycle should be matched with the phenological stage of the targeted plant (Markin and Yoshioka 1996). Studying the reproductive biology of gorse is important, not only for understanding its invasive behaviour, but also for undertaking control and management actions.

Findings

Our findings on four different aspects of the reproductive biology of gorse in South Australia and Sri Lanka indicate that the reproductive capacity of gorse differs in these two geographically distinct areas. Gorse populations in South Australia show markedly higher fruit set compared to the populations in Sri Lanka. During the time of the study, predation of pods was negligible in our study sites in both regions. However, we note that the findings for fruit:flower ratios and pod predation are more tentative since these parameter may have been confounded by differences in seasonality at the time of sampling. We found that gorse in Sri Lanka showed a higher number of seeds per pod compared to South Australian plants. We also found a significantly higher density of seeds under bushes in Sri Lanka. Our findings also revealed that the density of seeds was markedly lower three meters away from parent bushes. We found that more than 90% of gorse seeds germinated (before and after scarification), which is higher than has previously been found for fresh gorse seed scarified with acid (Sixtus *et al.* 2003).

Further research

A more comprehensive study is needed to investigate geographical variation in fruit:flower ratios of gorse. Since the fruiting phenology of gorse varies significantly between countries (Markin and Yoshioka 1996; Bowman *et al.* 2008), this aspect of study would need prolonged time. The variation in the longevity of the soil seed bank among different study sites of New Zealand (Hill *et al.* 2001), may provide an opportunity to investigate what factors contribute to the decline of gorse seed banks. The above study was not designed to investigate the causes of that variation; however, authors suggest that variation in innate seed dormancy and climate among sites may explain this difference. Pre-dispersal seed predation of gorse varies with several factors such as predator type, size of predator population and time of predation (Tarayre *et al.* 2007). Few studies have been conducted that investigate how predation changes temporally (Tarayre *et al.* 2007; Atlan *et al.* 2010). There are also insufficient studies to determine the intensity of predation needed to control gorse populations. If several predators are used in biological control programs, the balance or ratio of different predators that are needed also requires further study. Further studies of the germination of gorse seeds are also necessary to achieve a better understanding of how germination varies in nature with variation in factors such as soil depth, time after falling and light condition.

Comparative study of species distribution modelling of gorse (*Ulex europaeus*) in the Mount Lofty Ranges of South Australia and central highlands in Sri Lanka

Modelling the fundamental niche of species based on environmental parameters and known occurrence records is considered a powerful tool for predicting species’ potential distributions (Anderson *et al.* 2002). Understanding the potential distributions of invasive species is particularly important (Elith *et al.* 2010) due to the high risk they pose to the native biodiversity of other countries. Gorse is one of the most important invasive species in Australia which has been little studied using distribution modelling methods. Identification of geographic areas vulnerable to invasion by gorse would be important for making early actions to control the introduction or to potentially avoid further spread of this notorious species.

In ecological studies, it is often logistically infeasible that surveys can be conducted in all habitats to identify the presence or absence of a species. In this situation, SDM can be used to identify possible areas of distribution of a species and prioritize these areas for field surveys according to the suitability of prediction. Therefore, SDM is widely used today to identify probable areas of spread of invasive, threatened or other economically important species. However, due to historical restrictions, a species may not occupy all the suitable habitats predicted by the modelling exercise (Anderson *et al.* 2002) and the potential area predicted by the SDM may be over-estimated.

Findings

We did a modelling study to predict the distribution pattern of invasive gorse (*Ulex europaeus*) in two regions in its invasive range; South Australia and Sri Lanka. Our prediction using Maxent software for *U. europaeus* in South Australia found that the Mount Lofty Ranges and Kangaroo Island areas are predicted as high probability areas for gorse distribution.

The Maxent prediction does not include the Eyre Peninsula but does include scattered areas in the Yorke Peninsula. We observed how the Maxent prediction varied with a changing threshold value, i.e. a greater predicted area, comprising all of the Yorke Peninsula and a considerable part of the Eyre Peninsula, was obtained using the 'Minimum training presence' threshold criterion. We found that annual precipitation and yearly average aridity index contributed most to the *U. europaeus* model formulation. According to the prediction map and occurrence data distribution, we believe that gorse has acquired the majority of suitable areas in South Australia. Suitable areas for gorse in Sri Lanka are in the central highlands where gorse is currently distributed. The model suggested that the predicted areas for gorse in Sri Lanka are greater than area of its current distribution. However, full occupancy of a species' potential range is could be hindered due to geographic barriers, species interactions, behaviour, and lack of time for colonization (Elith 2000; Anderson *et al.* 2002;

Anderson 2003; Franklin 2009; Hortal *et al.* 2010). We found that the selection of environmental variables was very important and that climatic variables measured on a monthly basis did not perform well if the model was projected to a climatically distinct geographic area. The study successfully projected a model trained with invasive distribution data and applied to another geographic area.

Our comparisons of multiple SDM models for South Australia revealed that the Maxent prediction was relatively more conservative in comparison with the other three models, Bioclim, Domain and GLM, and therefore that the latter potentially over estimate the suitable climate space for gorse.

Further Research

Our study is limited to the distribution of gorse in South Australia and the projection of that model to Sri Lanka using presence-only data. However, it would be ideal to investigate other modelling algorithms that use presence-absence data and for comparison with our findings. A further area for study would be to develop more relevant species-specific variables using eco-physiological data for gorse.

Our study estimated the potential spread of *U. europaeus* under current climatic conditions; however, understanding the potential impacts of climate change on invasive species' distributions is significantly important for conservation planning (Webber *et al.* 2011). Therefore, a comprehensive worldwide study is needed to assess the potential distribution of *U. europaeus* under future climate change scenarios, ideally with both native and invasive range data, to investigate how this species' distribution may shift with changing climates. This may provide valuable information to enable weed managers to take early action to limit the spread of invasive gorse in affected countries.

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