Original article

Site-specific conditions influence plant naturalization: The case of alien Proteaceae in South Africa

Desika Moodley [a,b,*], Sjirk Geerts [a,b], Tony Rebelo [b], David M. Richardson [a], John R.U. Wilson [a,b]

[a] Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa
[b] Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch Research Centre, Claremont 7735, South Africa

ABSTRACT

The outcome of plant introductions is often considered in binary terms (invasive or non-invasive). However, most species experience a time lag before naturalization occurs, and many species become naturalized at some sites but not at others. It is therefore important to understand the site-specific mechanisms underlying naturalization. Proteaceae is an interesting case as some species are widespread invaders, while others, despite a long history of cultivation, show no signs of naturalization. At least 26 non-native Proteaceae species have been introduced to, and are cultivated in, South Africa. We mapped populations and examined differences between naturalized and non-naturalized populations (e.g. propagule pressure, land use and bioclimatic suitability). Of the 15 species surveyed, 6 were naturalized at one or more sites. Of these, *Hakea salicifolia* is most widely cultivated, but is only naturalizing in some areas (32 naturalized populations out of 62 populations that were surveyed). We found propagule pressure to be the most important determinant of naturalization for *H. salicifolia*. However, in suboptimal climatic conditions, naturalization only occurred if micro-site conditions were suitable, i.e. there was some disturbance and water available. For the other naturalized species there were few sites to compare, but we came to similar conclusions — *Banksia integrifolia* only naturalized at the site where it was planted the longest; *Banksia serrata* only naturalized at a site influenced by fire regimes; while *Banksia formosa* naturalized at sites with high propagule pressure, absence of fires and where there is no active clearing of the plants. Naturalization of Proteaceae in South Africa appears to be strongly mediated by site-specific anthropogenic activities (e.g. many planted individuals and water availability). More broadly, we argue that invasion biology needs to focus more closely on the mechanisms by which species and pathways interact to determine the likelihood and consequence of an invasion.

© 2014 Elsevier Masson SAS. All rights reserved.

1. Introduction

Only a subset of introduced species become naturalized and only a subset of naturalized species become invasive (Williamson and Brown, 1986). Different factors assume particular importance at different spatial scales and at different stages of the introduction-naturalization-invasion (INI) continuum (Blackburn et al., 2011; Richardson and Pyšek, 2012), but in general naturalization and invasion is the result of an interaction between species traits,

features of a site, and introduction dynamics. Each of these three factors has been studied in depth. For example, Pyšek and Richardson (2007) reviewed the influence of species traits; various features of a site have been studied [e.g. climate (Richardson and Thuiller, 2007), land use and human-mediated disturbance (Vilà and Ibáñez, 2011)]; while introduction dynamics such as propagule pressure (Colautti et al., 2006; Lockwood et al., 2005), and residence time (Wilson et al., 2007) have been the focus of many studies. However, fewer studies have explored the interactions between species traits, introduction dynamics, and features of a site.

Climatic suitability (an interaction between species traits and the prevailing climatic conditions at a site) is generally considered a prerequisite for naturalization and invasion (Guisan and Thuiller, 2005; Mack, 1996). However, introduction dynamics such as high propagule pressure can sometimes overcome barriers imposed by

suboptimal environmental conditions (Rejmánek et al., 2005b). Species introduced in large numbers over a long period of time have a greater chance of establishing and spreading than those with lower propagule pressure (Dehnen-Schmutz and Touza, 2008; Lockwood et al., 2005; Rouget and Richardson, 2003; Simberloff, 2009). In addition, plants occupying an area for a longer period have a greater chance to disperse more propagules, experience more favourable recruitment events and have a longer time for suitable phenotypes to be selected that can cope with local conditions (Pyšek et al., 2009; Rejmánek et al., 2005a).

One way to test these ideas is to examine the outcome of introducing several species to several localities in different ways (what has been termed a large unplanned natural experiment in invasion science). Along this line work on several model groups in plant invasion ecology, such as Australian acacias and *Pinus* species, has provided general predictors (Rejmánek and Richardson, 1996; Richardson et al., 2011). Here we use Proteaceae as a test case.

Proteaceae is a large family of flowering plants with a long history of introduction to many parts of the world, mainly for horticulture (Sedgley et al., 2007). Although evidence from around the world suggests that Proteaceae is not a particularly "weedy" family (only 8 species of the 402 introduced species are recorded as invasive; Moodley et al., 2013), this may be due at least partly to the fairly recent history of introductions for many species. These recently introduced species are not yet invasive but might form part of the "invasion debt" (Essl et al., 2011). Given that many species have been introduced to many localities and these species occupy different stages in the invasion continuum, Proteaceae provides an excellent group to identify possible site-specific factors that are likely to drive biological invasions. Because of the growing commercial interest, there is also a need for post-border risk assessments in this group (Wilson et al., 2013).

South Africa in particular has a substantial number of alien Proteaceae (hereinafter referred to as proteas), which were introduced for use as barrier plants, ornamental purposes, food, cut-flowers and as landscape plants. At least 26 proteas have been introduced into South Africa (SAPIA, accessed November 2011; Rebelo, 1991–2001; pers. obs.) of which 11 species are recorded as naturalized (Fig. 1). Three of these species (*Hakea drupacea* (C.F.Gaertn.) Roem. & Schult., *Hakea gibbosa* (Sm.) Cav., and *Hakea sericea* Schrad. & J.C.Wendl.) have become widespread invaders in South Africa, although in each case there are still climatically suitable areas of the country that are not yet invaded (Le Maitre et al., 2008; Richardson et al., 1987; Rouget et al., 2004).

For other naturalized proteas we are beginning to understand the drivers of invasion, which include the presence of a suitable fire regime (Geerts et al., 2013). In addition, many species are extensively cultivated (i.e. high introduction efforts) but have not yet become naturalized. For example, South Africa is one of the largest producers of macadamia nuts in the world and has for many years been home to large plantations of *Macadamia integrifolia* Maiden & Betche, *M. tetraphylla* L.A.S. Johnson and cultivars of these species (Mabiletsa, 2004; Nagao, 2011; The Southern African Macadamia Growers' Association, http://www.samac.org.za), but there are no records of the genus naturalizing in southern Africa (SAPIA, accessed May 2013). The seeds of these species are dispersed by water (Department of Sustainability, Environment, Water, Population and Communities (2013), http://www.environment.gov.au/sprat). Therefore the location of these plantings (gardens and orchards) may be preventing its spread. This suggests that there is potential for future naturalization since these species may be in a lag phase. Finally, evidence is emerging that some introduced Proteaceae species with a long history in South Africa are starting to become naturalized, but only at a few sites. For example, anecdotal observations suggest that *Hakea salicifolia* (Vent.) B.L. Burtt, a species widely planted as a hedge plant for at least a century, is starting to spread.

Of the naturalized Proteaceae in South Africa, *H. salicifolia* is intermediate in its adventive distribution. The species was for many years considered non-invasive. It was not listed among 84 "emerging invaders" in a national study that aimed to prioritize alien plant species and areas for management action (Nel et al., 2004). Although not listed under current legislation, it has been considered for listing, and therefore an assessment of the threats it poses is overdue (Wilson et al., 2013).

H. salicifolia has a wide planted distribution in South Africa where it is used as a hedge plant and for windbreaks across the fynbos, grassland and savanna biomes. It has naturalized and become invasive in several regions of the world (Table 1). It is an obligate seeder and possesses follicles that afford some protection for the seeds against fire (Protea Atlas Database). In New Zealand fires have successfully assisted the spread of *H. salicifolia* (Williams, 1992). However, in South Africa the lack of spread into fynbos vegetation has been attributed to thin follicle walls that are unable to protect seeds from typical fynbos fires (Richardson et al., 1987).

This study aimed to (1) determine the invasion status of introduced Proteaceae species in South Africa which are not classified as major invaders; (2) conduct a qualitative assessment of factors explaining naturalization for Proteaceae species in South Africa; and (3) quantitatively analyse factors that predict naturalization for species that have many naturalized and non-naturalized populations (*H. salicifolia* being the only example with sufficient data for detailed analysis).

2. Methods

2.1. Study sites

We compiled a list of all recorded localities of alien proteas in southern Africa, using the Protea Atlas Database and the Southern African Plant Invaders Atlas (SAPIA) as initial sources (SAPIA, accessed November 2011; The Protea Atlas Project, accessed August 2011). Following detailed field searches we also added personal observations and information provided by farmers and land owners to the locality list. Our aim was to understand which site factors are important for triggering naturalization (i.e. transition from introduction to naturalization; Richardson and Pyšek, 2012); we therefore excluded *H. drupacea*, *H. gibbosa*, and *H. sericea*. It is illegal to
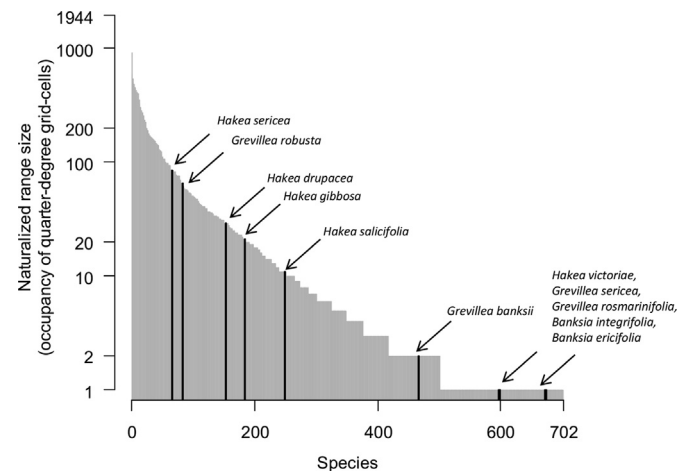

Fig. 1. Ranked bar plot showing the naturalized range sizes of alien plants in South Africa (log scale) with naturalized Proteaceae highlighted in black. The data were derived from the SAPIA database, accessed November 2011.

Table 1
Introduced Proteaceae species recorded in South Africa and populations surveyed in this study. Three major invaders in South Africa (*Hakea drupacea*, *H. gibbosa* and *H. sericea*) were excluded from the list. For a full list of introduced Proteaceae in South Africa and worldwide see Moodley et al. (2013).

Species	Number of sites recorded from databases	Number of surveyed sites in this study	Number of naturalized sites detected in this study	Invasion status elsewhere
Banksia baxteri	2	0	NA	Not recorded as naturalized
B. coccinea	3	3	0	Not recorded as naturalized
B. ericifolia	15	15 (only 5 populations were found)	2	Naturalized in New Zealand[a]; invasive in South Africa[b]
B. formosa	4	4	2	Naturalized in Australia[a,d]
B. hookeriana	3	1	0	Not recorded as naturalized
B. integrifolia	9	9	1	Naturalized in New Zealand[a], Azores[c] and Australia[d]; invasive in Hawaii[e], beginning to invade in Kleinmond in the Western Cape, South Africa (this population has been cleared)[f]
B. prionotes	1	1	0	Not recorded as naturalized
B. serrata	1	1	1	Naturalized in New Zealand[a]
B. speciosa	7	4	0	Not recorded as naturalized
B. sphaerocarpa	1	0	NA	Not recorded as naturalized
B. spinulosa	2	2	0	Naturalized in Australia[a]
Grevillea banksii	18	0	NA	Not recorded as naturalized
G. juniperina	1	0	NA	Not recorded as naturalized
G. robusta	197	46	1	Invasive in South Africa[g,h], Hawaii, Brazil, Uganda and Guatemala[h], Reunion island[i], and many pacific islands[e]
G. rosmarinifolia	1	0	NA	Not recorded as naturalized
G. sericea	1	0	NA	Not recorded as naturalized
Hakea petiolaris	1	1	0	Not recorded as naturalized
H. salicifolia	133	62	32	Naturalized in New Zealand[a,j], South Australia, Victoria and Tasmania[a,d,k], France, Spain and Portugal[c,l], South Africa[a], Swaziland[m] and South India[n]; Invasive in Portugal, New Zealand and Australia[h]
H. victoriae	3	0	NA	Not recorded as naturalized
Macadamia integrifolia	3	2	0	Naturalized in Paraguay, New Zealand, Puerto Rico, United States[a] and Australia[d]
M. tetraphylla	2	2	0	Naturalized in Paraguay, New Zealand, Hawaii[a] and in Australia[d]
Stenocarpus sinuatus	2	0	NA	Not recorded as naturalized
Telopea speciosissima	2	2	0	Naturalized in Australia[a]

[a] Global compendium of weeds, http://www.hear.org/gcw, accessed March 2012.
[b] Geerts et al. (2013).
[c] Delivering Alien Invasive Species Inventories for Europe, www.europe-aliens.org, accessed November 2011.
[d] Randall (2007).
[e] Pacific Island Ecosystems at Risk (PIER), http://www.hear.org/pier, accessed November 2011.
[f] University of Cape Town, Bolus herbarium collection.
[g] Southern African Plants Invaders Atlas, accessed March 2012.
[h] Richardson and Rejmánek (2011).
[i] C. Lavergne (pers. comm).
[j] Williams (1992).
[k] Atlas of Living Australia, http://www.ala.org.au, accessed August 2012.
[l] Tutin (1993).
[m] Henderson (2007).
[n] Matthew (1999).

cultivate any of these major invaders in South Africa and there are few, if any, cultivated populations left regardless of whether these populations had naturalized or not. We did, however, include *Grevillea robusta* A.Cunn. ex R.Br., because although it is widely planted, it is not considered a widespread invader in South Africa.

This resulted in a list of 411 alien protea localities in southern Africa (see Table 1 for species and localities mapped). For *H. salicifolia* and *G. robusta*, which are widely planted in South Africa, we selected sites across the distribution ranges of the species since it was not feasible to visit all sites. For the *Banksia* populations we were able to visit most of the recorded sites. On visiting each site, we assessed whether populations had the opportunity to spread (i.e. where plantings adjoin potentially invasible habitats; Fig. 2). If spread was possible we surveyed the site in more detail. For example, a single individual planted in a parking lot surrounded by paved roads, has no chance of spreading, whereas a plant growing next to an abandoned field has the opportunity to spread.

Preliminary surveys suggested few naturalized populations for all species except *H. salicifolia* (Table 1), and so *H. salicifolia* was selected for more detailed analysis.

2.2. Survey methods

At each site plants were mapped using a hand-held GPS. Each site was systematically surveyed on foot at least 10 m from any plants observed (in most cases plants could be seen much further than 10 m away). Recruiting individuals were measured and categorized as seedlings (<300 mm in height); juveniles (>300 mm, non-reproducing plants); and adults (>300 mm, reproducing plants). At five sites with extensive recruitment, the number of plants was estimated by walking around the population to delimit the extent of the population; placing transects through a part of the population that most accurately depicted the density and size classes; and counting all seedlings, juveniles and adults.

Fig. 2. Situations depicting sites where species can and cannot spread in the Western Cape. (A) An urbanized setting which shows *Grevillea robusta* in a parking lot with no chance of spread (Stellenbosch); (B) *Banksia integrifolia* in gardens where plants can spread into natural fynbos (Pringle Bay); (C) *Hakea salicifolia* hedge with potential to spread into an abandoned orchard (Grabouw). Photographs: D. Moodley.

Following the scheme proposed by Richardson et al. (2000) and Pyšek et al. (2004), we classified populations as naturalized when self-sown adult plants were present (this also includes invasive populations where plants have spread more than 100 m within 50 years) and as non-naturalized populations when no self-sown adult plants were detected. There is no guarantee that self-sown juvenile plants will reach maturity and form self-reproducing adult plants — these plants may remain as casual aliens (Richardson and Pyšek, 2006). Therefore, although we surveyed populations comprising juvenile plants as the oldest recruiting individuals, these populations were classified as non-naturalized.

2.3. Quantitative analysis of the invasion success of H. salicifolia

At each site we assessed a variety of site-specific predictor variables (Table 2). These variables were selected based on the results of previous studies that assessed the role of different factors in mediating naturalization. In addition to variables commonly used in other studies (i.e. height of a plant and seed output), we included soil data because Australian proteas grow mostly in soils with low-nutrient content and low pH (Myerscough et al., 2001). Quantitative analyses were only conducted for *H. salicifolia* populations because of the small sample size of other surveyed species. We first screened pair-wise correlations between predictor variables to avoid including correlated variables in the model (Fig. S1, Kendall rank correlation coefficient <0.65). Accurate fire records were only available for two *H. salicifolia* populations and we could not determine the dates of the last fires at other sites. Because time since last fire was strongly correlated with other predictors (i.e. total number of planted trees, height, total area of spread and biome) we excluded this variable from the model. While the number of planted individuals in a population and seed output were correlated (r ~0.65), both were retained in the model due to the clear demonstration of the importance of propagule pressure in many plant invasion studies.

2.4. Bioclimatic modelling

Species distribution modelling offers a method to predict potential invasive distributions and thereby aid both risk assessments and reduce survey costs by allowing efforts to be focussed on high risk areas (Elith and Leathwick, 2009; Kaplan et al., 2014; Webber et al., 2011; Zengeya et al., 2013). To determine the bioclimatic preferences of *H. salicifolia* in its introduced range, we developed a species distribution model using MaxEnt version 3.3.3e (Phillips et al., 2006). This is a correlative approach that uses the relationship between environmental variables and presence-only records to predict potentially suitable areas for a particular species (Elith et al., 2011; Warren and Seifert, 2011). This technique has been widely used because of its high predictive accuracy (Aguirre-Gutiérrez et al., 2013; Baldwin, 2009; Elith et al., 2011; Phillips and Dudík, 2008).

2.4.1. Distribution records

H. salicifolia comprises two subspecies with overlapping native ranges: *H. salicifolia* subsp. *salicifolia* and *H. salicifolia* subsp.

Table 2
Description of predictor variables and methods used to obtain data for alien Proteaceae in South Africa.

Predictor variable	Methods of measuring	References
Elevation	GPS	
Age[a]	Counted the number of whorls for *Banksia* species	Jenkins et al. (2005)
	Height was a measure of age for *Grevillea robusta* (cm). We used a crude estimate of age by counting the growth rings of a single plant (800 cm)	T. Mullin (pers. com.)
	Measured stem diameter using callipers for *Hakea salicifolia* (cm). Williams (1992) provided age estimates based on stem diameter and the proportion of open and closed follicles	Williams (1992)
Propagule pressure	Total number of planted individuals	
Propagule rain	For each population, seed output was estimated by counting all the follicles on one planted individual and multiplying it by the number of seeds (always 2 winged seeds per follicle) and individuals. If the population comprised plants of different heights, we counted seed output for each height class. In each population 10 follicles were randomly selected for seed count to confirm two seeds per follicle as in its native habitat.	
Height	Estimated height (mm)	
Total area of spread	Polygons were constructed in ArcGIS 10.1 to measure the total area of a spreading population.	
Time since last fire*	Indicator species: age of re-seeding native Proteaceae	
Land use	Considered which land types are adjacent to the populations (in many cases there are more than one land use type)	
Management	Whether plants are cut or irrigated	
Biome	ArcGIS 10.1 was used to identify biomes	Mucina and Rutherford (2006)
Soil pH	Weighted average of pH values	Harmonized World Soil Database (2009)
Soil drainage	Drainage classes	Harmonized World Soil Database (2009)

[a] Where possible we tried to get information from farmers or land owners.

angustifolia (A.A.Ham.) W.R.Barker (Flora of Australia online, at http://www.environment.gov.au/biodiversity/abrs/online-resources/flora/main/index.html). These taxa differ in the width of their leaves; >7 mm for subsp. *salicifolia* and 4–7 mm for subsp. *angustifolia* (New South Wales Flora online at http://plantnet.rbgsyd.nsw.gov.au). Using callipers we carried out ad hoc measurements of leaves on older branches and only observed plants with leaves >7 mm in width. Based on morphology, we suggest that only subsp. *salicifolia* has been introduced, corroborating this, only subspecies *salicifolia* has been recorded as a widely introduced species, whereas subspecies *angustifolia* has not yet been recorded outside its native range (PlantNET - Flora of New South Wales, at http://plantnet.rbgsyd.nsw.gov.au/floraonline.htm).

Because *H. salicifolia* does not have a wide invasive range in South Africa, we extracted geo-referenced distribution records from its native range (Atlas of Living Australia, www.ala.org.au, accessed May 2012). Records were scrutinized for synonyms, subspecies, missing coordinate data, spatial uncertainty, points in the ocean and duplicated locality points which we omitted. A total of 157 occurrence records were used to build the model.

2.4.2. Background selection

MaxEnt requires a defined region to obtain background data. Background data informs the model of environmental conditions where the species could be present (but has not been recorded), therefore background selection is an important method and can influence the results (Elith et al., 2011; VanDerWal et al., 2009). The Köppen−Geiger climate classification was used to define the background points. Following recommendations by Elith et al. (2011) and Webber et al. (2011), we restricted the background to Köppen−Geiger polygons that contained one or more records of *H. salicifolia*. We then created 10,000 background points by sampling random points within the defined environmental mask.

2.4.3. Bioclimatic variables

Environmental data on 30 arc-second resolution grids were downloaded from the WorldClim database (www.worldclim.org, accessed June 2012). We observed that populations located in drier habitats die easily if they are not watered regularly. Thus, precipitation during the dry months is necessary for *H. salicifolia* to survive (pers. comm. with landowners). Therefore, we selected precipitation of the driest quarter as a primary predictor variable and subsequent variable selection was based on predictors with the lowest pair-wise correlations (Kendall rank correlation coefficient <0.65). This approach resulted in two rainfall (precipitation of the driest quarter and precipitation of the wettest quarter) and two temperature (maximum temperature of the warmest month and mean temperature of the coldest quarter) variables.

2.4.4. Modelling technique

The model was run using default parameters: 'logistic output', 'jacknife measures of variable importance', 'clamping' and a regularization value of 1 to reduce over-fitting. The data splitting procedure was replicated 10 times using k-fold cross-validation, in each model, all records were partitioned into a training set (calibration) and a testing test (evaluation) (Phillips et al., 2006). The test points are a random sample taken from the species presence localities. The 'random seed' option was selected so that a different training and test sample is randomly generated each time the model is replicated. In addition, only 'hinge features' were used to fit the model since this allows for smoother response curves that are ecologically relevant (Elith et al., 2010). The different models that were calibrated in the native range were then projected to the introduced range in South Africa to identify areas with potentially suitable climatic conditions.

The minimum training presence (MTP) logistic threshold or lowest-presence threshold, which describes the lowest probability associated with the presence of a species, was selected to define climatically suitable regions (Pearson et al., 2007). To produce a binary map using ArcGIS 10.1, we displayed all unsuitable regions as white to grey (values below the average MTP), suitable regions as green (average MTP value), moderately suitable as yellow (probability value of 0.5) and highly suitable as red (probability value of 1). The predictive power of the model was examined using the area under the receiver operating characteristic curve (AUC; Hanley and McNeil, 1982). We also mapped known introduction records onto the projected map to assess the potential range of *H. salicifolia* in South Africa.

2.5. Statistical analysis

The analyses were performed in two stages, first using all surveyed *H. salicifolia* populations ($n = 62$). Here we found that a large proportion of source populations occur in regions with suboptimal climates which suggests that climate could be important in determining observed patterns of naturalization. To further explore the factors influencing naturalization, for the second part of the analysis we only used sites in climatically suitable regions (using the minimum presence threshold).

The data were analysed using generalized linear models (GLM) with binomial errors to test the significance of factors influencing the likelihood of populations naturalizing. The response variable was coded as 1 for naturalized populations and 0 for non-naturalized populations. All analyses were performed in R version 2.15.1 (R Development Core Team, 2009).

3. Results

Fifteen species of proteas comprising 145 populations were surveyed across South Africa (Table 1). All species except *G. robusta* and *H. salicifolia* were recorded only in the Western Cape province. During our surveys we found two species, *Banksia formosa* and *Banksia serrata*, that were not recorded in our database, but which were spreading. Several new *Banksia integrifolia* populations were also discovered, and one population in Pringle Bay is successfully invading (*sensu* Pyšek et al., 2004).

Of all introduced proteas in South Africa, the genus *Banksia* L.f. has the greatest number of introduced species (11 species). *Banksia* species are planted for their use as cut-flowers and make excellent windbreaks. *G. robusta* is also planted as windbreaks in South Africa and has the widest global invasive range of any species of Proteaceae (Moodley et al., 2013; Richardson and Rejmánek, 2011). There are a few records of *Macadamia* species and *Telopea speciosissima* (Sm.) R.Br. that are no longer under cultivation in South Africa; these species are typically planted for food and as ornamentals, respectively (Moodley et al., 2013).

We recorded 117 *H. salicifolia* populations with a wide planted distribution throughout South Africa, from Nieuwoudtville in the Northern Cape to Thohoyandou in Limpopo. Sixty-two populations were surveyed: 32 were naturalized and 30 non-naturalized (*sensu* Pyšek et al., 2004).

The species distribution models developed for *H. salicifolia* performed well. The average test AUC for the predictive models of 141 training and 16 testing occurrence data was 0.987 ± 0.003 (±standard deviation; see Table S1 for further details). This shows the model has excellent predictive power (Swets, 1988). Among the four climatic parameters, precipitation of the driest quarter was the most influential predictor followed by precipitation of the wettest quarter (Table S2). In addition, the response curves of the two most influential predictors indicate that *H. salicifolia* has a greater occurrence
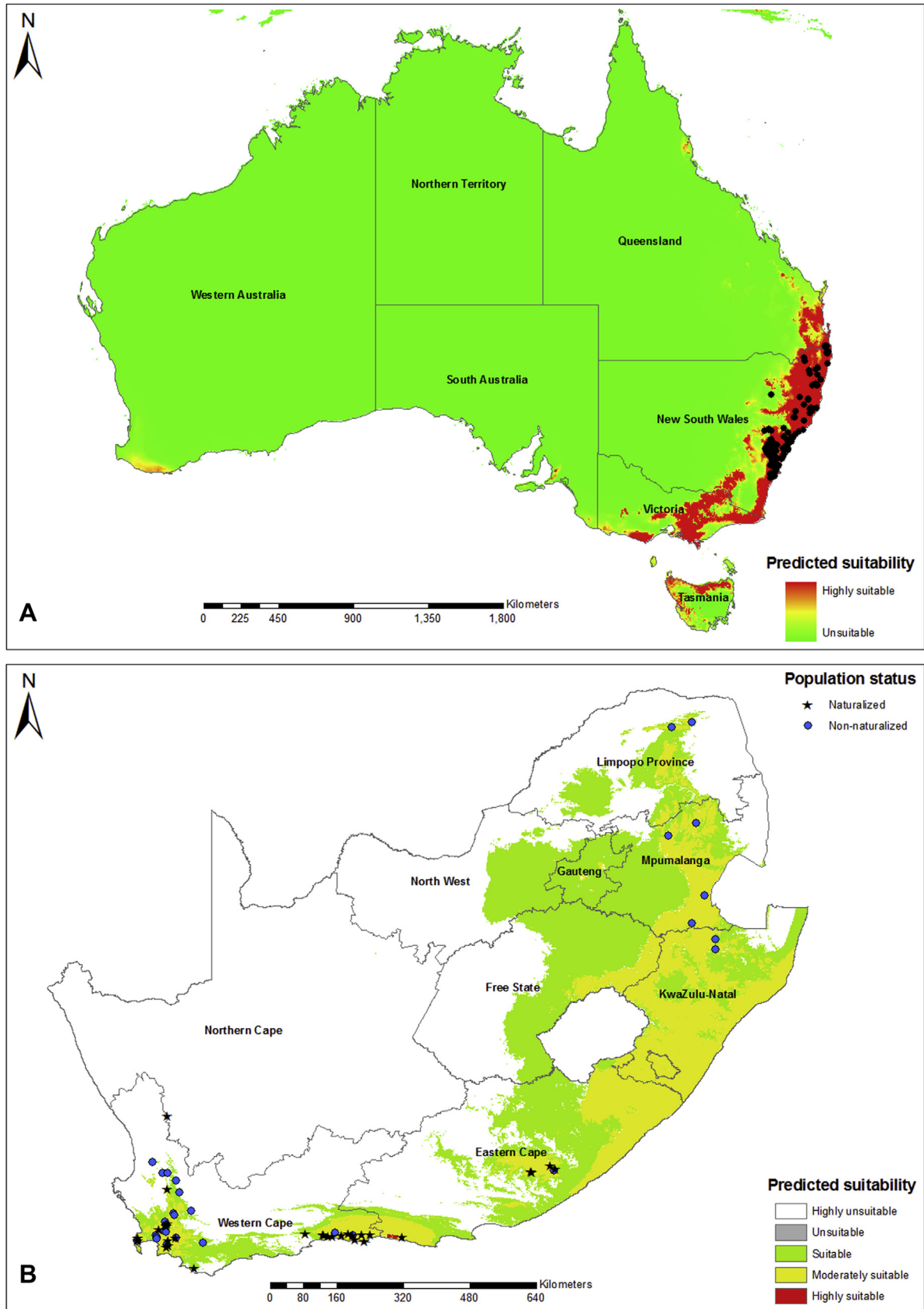
Fig. 3. Bioclimatic suitability of *H. salicifolia* subsp. *salicifolia* in (A) its native range in Australia with native distribution records, and (B) across its introduced range in South Africa. Native distribution data was obtained from the Atlas of Living Australia, http://www.ala.org.au and introduced records were sourced from the SAPIA and the Protea Atlas Project databases.

probability in regions with high rainfall (Fig. S2). If similar factors influence naturalization in the species' introduced range, it might be expected that *H. salicifolia* is restricted by precipitation in South Africa.

Highly suitable regions for *H. salicifolia* in it native range includes the eastern Australian coast and northern Tasmania (Fig. 3A). Climate suitability is generally poor for *H. salicifolia* in South Africa as suitability scores are low (most values <0.1 and highest suitability = 0.6). A striking observation is the distribution pattern of planted populations and predicted suitability (Fig. 3B). This can be used to validate good model performance. It is also evident that *H. salicifolia* has not yet filled its potential niche. The greatest numbers of planted *H. salicifolia* populations occur in the Western Cape which was predicted to have low climatic suitability (Fig. 3B). In contrast, *H. salicifolia* is not widely planted in regions with climatic conditions most similar to those in the native range. Populations in the Highveld region are few and non-naturalized. The only region with high climatic suitability and a large number ($n = 14$) of planted populations is the George-Knysna region in the southern Cape and a small area in the Eastern Cape, where 13 populations (93%) are naturalized.

Using all surveyed *H. salicifolia* populations, the number of seeds in a population (used as a proxy for propagule pressure) differed significantly between naturalized and non-naturalized populations (Fig. 4A; Table S3A). Populations with larger canopy-stored seed banks were more likely to naturalize ($z = 2.311$, $P = 0.020$, 95% CI = 0.062 to 0.508, a small difference between the CI indicates precise estimates while wide intervals show less precision).

Similar to the full data set, only one variable was found to be associated with naturalization in the climate-informed analysis: the number of seeds in a population (i.e. propagule pressure; Fig. 4B; Table S3B). Populations with greater numbers of seeds were more likely to have naturalized ($z = 2.037$, $P = 0.034$, 95% CI = 0.047−0.520). In contrast, there was no significant effect of the number of seeds at climatically unsuitable sites ($z = 0.739$, $P = 0.460$, 95% CI = −0.306 to 4.783; Table S4), although equally there was also no significant difference in the number of seeds between climatically suitable and unsuitable sites ($z = −0.607$, $P = 0.544$, 95% CI = −4.438 to 0.563; Table S4).

Land use did not emerge as a significant determinant of naturalization in *H. salicifolia*. There is evidence that this species can naturalize in all areas where it is planted, particularly in disturbed sites (Fig. S3). *H. salicifolia* is widely used for wind breaks which are on the edge of fields and therefore, often next to roads. Thirty-nine percent of populations occurred along roads and many of these populations are naturalized. Naturalization was also observed in natural vegetation, though only at one of seven sites where planted individuals bordered natural vegetation.

4. Discussion

Our results provided a clear example of the conditional nature of invasions, with different factors driving naturalization of different species at different sites. In particular, species have to be given the right conditions for establishment and spread. For *H. salicifolia* we were able to elucidate the factors that mediate naturalization and found that suitable climatic conditions and high propagule pressure were significant drivers of naturalization. We found that *H. salicifolia* can also naturalize in regions with suboptimal bioclimatic conditions if conditions are ameliorated through human activities that provide additional water and disturbance.

4.1. Site factors influencing the invasion status of H. salicifolia

There is a mismatch between the observed planted distribution of *H. salicifolia* and the area that is defined as bioclimatically

suitable based on records from the native range. Although there are various well known methodological issues with species distribution models (e.g. Elith and Leathwick, 2009; Heikkinen et al., 2006; Rodríguez-Castañeda et al., 2012), this result is likely to be robust. *H. salicifolia* is widely planted in the winter-rainfall region of South Africa (Fig. 3B), but in its native range summer-rainfall dominates (Fig. 3A). By comparison where *H. salicifolia* is planted in areas with a rainfall regime similar to SE Australia (e.g. the southern Cape from George to Port Elizabeth), the rate of naturalization is very high (~90% of populations surveyed).

Seed output (a proxy for propagule pressure) was a significant driver of naturalization. This suggests that if *H. salicifolia* is planted more widely in climatically suitable areas, populations would have the ability to successfully overcome barriers to naturalization. Human-mediated propagule pressure is therefore a crucial determinant of invasions in this case.

4.2. Qualitative assessment of factors influencing naturalization

Where the broad-scale climate is unsuitable, naturalization appears to be limited to sites with disturbance, e.g. along roadsides (Fig. 5A); hedges under pine plantations (Fig. 5B); steep slopes; seepage areas; and high propagule pressure (Fig. 5C) and localities that receive additional water from human activities such as agriculture (Fig. 5D). Therefore, we predict that naturalizations in climatically unsuitable areas will not result in widespread invasive populations, but will remain fairly restricted and local.

The fact that most plantings of this species have been in regions with suboptimal climatic conditions, and perhaps also because the thin-walled follicles of this species provide inadequate protection of the seeds against fynbos fires (Richardson et al., 1987), most likely explains why it has not yet become a major invader. We did find one population spreading after a fire, suggesting that canopy-stored seeds are able to survive fires in some situations.

Disturbance, in particular fire, appears to be important for successful naturalization of other alien proteas in South Africa. After a fire in 2010 (Cape Nature, 2011), a stand of nine *B. serrata* trees planted in natural fynbos in Betty's Bay approximately 14 years previously, is now well established with at least 10 seedlings, 34 juveniles and 11 mature trees. Similarly, invasions by *Banksia ericifolia* appear to have been stimulated by exposure to natural fire regimes (Geerts et al., 2013). In contrast, two of the four *B. formosa* populations (a non-serotinous species) appear to be spreading despite a lack of fire. The two spreading populations are planted in large numbers for use as cut-flowers in a flower farm in Elim. Due to a lack of fire, substantial propagule pressure and no active clearing of plants at these two sites, massive recruitment is occurring (at least 9000 mature plants were recorded in one population and 7 in the other).

Three of the *Banksia* species which are strongly serotinous (*B. serrata*, *B. ericifolia* and *B. integrifolia*) as well as *H. salicifolia* which is weakly serotinous are adapted to fire (i.e. serotinous cones release seeds after fire). However, these species are mainly grown in situations where fire is excluded. *Banksia* species are grown in flower farms and *H. salicifolia* is used as a hedge. These uses protect the plants from fire when the surrounding vegetation burns. Consequently, these species may be in a lag phase because of the absence of a key requirement for their recruitment (fire), so that seed release due to death of plants is not synchronized to veld that is suitable for seedling establishment. Invasion may be triggered when a bush fire should reach and affect the cultivated plants, resulting in post-fire seed release into natural veld during its seedling establishment phase.

If a fire-adapted species is not exposed to fire then recruitment is dependent on old or dying plants. Therefore, the longer the
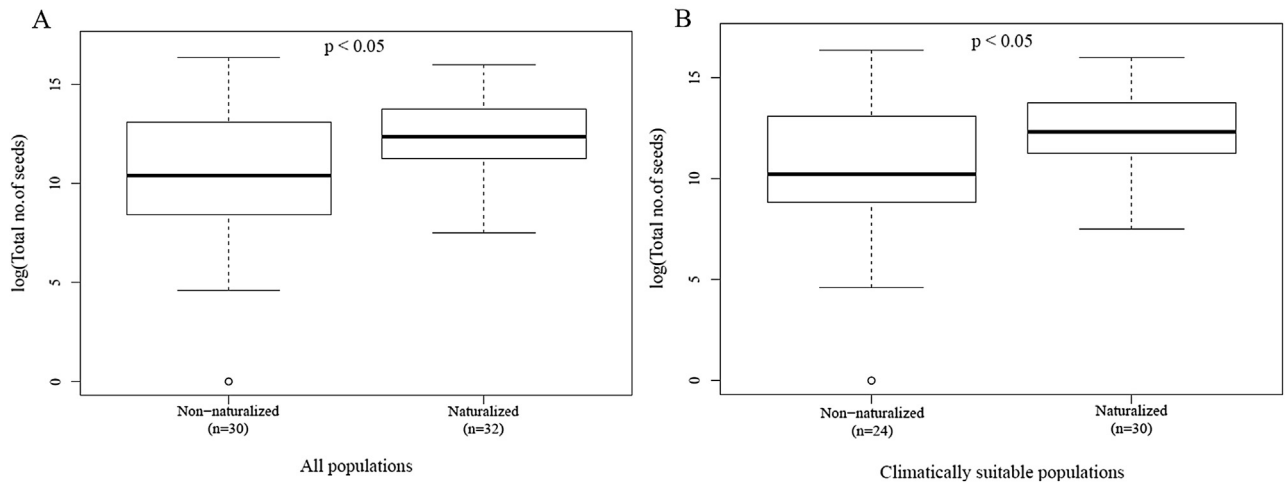
Fig. 4. Relationship between the number of seeds in *H. salicifolia* populations and naturalized and non-naturalized plantings across South Africa at (A) all planted sites ($n = 62$) and (B) climatically suitable sites ($n = 54$). Box plots display median, 25th and 75th percentiles, and data range. Open circles indicate outliers.

residence time for a serotinous species, the greater the chance of recruitment. A long residence time provides an explanation for the spread of *B. integrifolia*. A single *B. integrifolia* tree was planted as an ornamental plant in Pringle Bay 33 years ago (landowner, pers. comm.). This is now an invasive population with several seedlings, juveniles and mature plants spread across a distance of 253m from the founder tree into natural vegetation. All other populations are much younger and are not yet spreading. These cases demonstrate that fine-scale determinants are important triggers of naturalization in this group and that naturalization at regional scales occurs when populations are given opportunities to spread (i.e. conditional invasions).

5. Management recommendations

From this study we suspect that *H. salicifolia* will not become a major problem where it is widely planted in areas with winter-rainfall. But plantings in summer-rainfall regions (e.g. Limpopo, Mpumalanga and KwaZulu-Natal) have a high risk of producing invasive populations. In the southern Cape such as the Knysna region which experiences rainfall all year round, and has suitable climatic conditions as well as many naturalized populations, *H. salicifolia* plantings should be prohibited, and existing plantings removed. The fact that *H. salicifolia* is widely planted in winter-rainfall regions but is likely to become invasive if planted in regions with azonal or summer-rainfall creates a potential conflict of interest with costs and benefits varying spatially. For this reason, *H. salicifolia* should ideally be regulated in South Africa according to rainfall zones, and in particular should be banned in parts of the country with all year round or summer-rainfall.

We also recommend that other alien proteas be managed on a case by case basis in consultation with relevant stakeholders. Species which are naturalizing at only a few sites may be appropriate targets for nation-wide eradication. But if stakeholders

Fig. 5. Potential reasons for naturalization of *H. salicifolia* in areas predicted to be climatically unsuitable: (A) Plants spreading along a disturbed road verge (Paarl, Western Cape); (B) hedge planted adjacent to a pine plantation and spreading under the pines (Tokai, Cape Town, Western Cape); (C) a population planted in a semi-circular manner around a graveyard, with massive recruitment (Paarl, Western Cape); and (D) naturalization next to an irrigation system (near Piketburg, Western Cape).

consider certain species to have substantial commercial (or cultural) value, then regulation may be required. Management practices should be developed (e.g. avoid planting serotinous species in areas prone to natural fires) and all plantings should be monitored so that invasions and impacts can be limited.

6. Conclusions

Only 8 Proteaceae species are currently recognized as invaders globally (Moodley et al., 2013; Rejmánek and Richardson, 2013), but due to the commercial interest in this family (e.g. species used for ornamental purposes, windbreaks and cut-flowers), risk assessments are necessary to prevent another wave of widespread invaders. Risk assessments are an important tool to identify potentially invasive species and assist in prioritizing management efforts of naturalized species, but management needs to be adaptive (Hulme, 2012). This paper has demonstrated the value of site-specific assessments in providing a more complete picture of the risks of introduced species.

Our results confirm the crucial importance of introduction dynamics (in this case propagule pressure) as a driver of invasions, but also show that this factor interacts in a complex way with site factors and species traits. As shown for *Metrosideros excelsa* (Myrtaceae) in fynbos (Rejmánek et al., 2005b), high propagule pressure can produce invasions of alien proteas even in conditions that are suboptimal for growth and recruitment. With *H. salicifolia*, if the broad-scale climate was not suitable, populations could still naturalize if the local conditions were favourable, although these populations are fairly restricted. For many of the fire-adapted proteas, a suitable fire regime appears to be a prerequisite.

Risk assessments are important for developing permitted and prohibited lists. Such lists are used to restrict the introduction of species which have an unacceptable invasion risk (Dehnen-Schmutz, 2011). One criterion of risk assessments, and a good predictor of invasiveness, is whether a species is invasive elsewhere (Herron et al., 2007; Reichard and Hamilton, 1997). This serves as an indication of whether species should or should not be placed on a permitted list. Consequently, *H. salicifolia* should not appear on any permitted lists due to its opportunistic invasive nature. This species has the potential to escape cultivation and become invasive under favourable conditions (i.e. summer-rainfall regions and high propagule pressure), and in regions that are climatically unfavourable but where naturalization is facilitated by site-specific conditions (i.e. available water). Assessing site-specific factors across a range of climates provides insight on the general mechanisms facilitating invasions and assists in providing management recommendations that are adapted for each region.

Appendix A. Supplementary data

Supplementary data related to this article can be found at doi:10.1016/j.actao.2014.05.005.

References

Aguirre-Gutiérrez, J., Carvalheiro, L.G., Polce, C., van Loon, E.E., Raes, N., Reemer, M., Biesmeijer, J.C., 2013. Fit-for-purpose: species distribution model performance depends on evaluation criteria – Dutch hoverflies as a case study. PLoS One 8, e63708.

Baldwin, R.A., 2009. Use of maximum entropy modeling in wildlife research. Entropy 11, 854–866.

Blackburn, T., Pyšek, P., Bacher, S., Carlton, J., Duncan, R., Jarošík, V., Wilson, J., Richardson, D., 2011. A proposed unified framework for biological invasions. Trends Ecol. Evol. 26, 333–339.

Cape Nature, 2011. All Recorded Fires on CapeNature Managed Property. Western Cape Nature Conservation Board (WCNCB) and Scientific Services.

Colautti, R.I., Grigorovich, I.A., MacIsaac, H.J., 2006. Propagule pressure: a null model for biological invasions. Biol. Invas. 8, 1023–1037.

Dehnen-Schmutz, K., 2011. Determining non-invasiveness in ornamental plants to build green lists. J. Appl. Ecol. 48, 1374–1380.

Dehnen-Schmutz, K., Touza, J., 2008. Plant invasions and ornamental horticulture: pathway, propagule pressure and the legal framework. In: Floriculture, Ornamental and Plant Biotechnology Advances and Topical Issues. Global Science Book, U.K., pp. 15–21.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1, 330–342.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43–57.

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Hülber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., Vilà, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.-L., Roques, A., Pyšek, P., 2011. Socioeconomic legacy yields an invasion debt. Proc. Natl. Acad. Sci. USA 108, 203–207.

FAO/IIASA/ISRIC/ISSCAS/JRC, 2009. Harmonized World Soil Database. FAO/IIASA, Rome, Italy/Luxemburg, Austria.

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

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143, 29–36.

Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W., Sykes, M.T., 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Prog. Phys. Geogr. 30, 751–777.

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

Herron, P.M., Martine, C.T., Latimer, A.M., Leicht-Young, S.A., 2007. Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England. Divers. Distrib. 13, 633–644.

Hulme, P.E., 2012. Weed risk assessment: a way forward or a waste of time? J. Appl. Ecol. 49, 10–19.

Jenkins, M.E., Morrison, D.A., Auld, T.D., 2005. Use of growth characteristics for predicting plant age of three obligate-seeder Proteaceae species. Aust. J. Bot. 53, 101–108.

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

Le Maitre, D.C., Thuiller, W., Schonegevel, L., 2008. Developing an approach to defining the potential distributions of invasive plant species: a case study of Hakea species in South Africa. Global Ecol. Biogeogr. 17, 569–584.

Lockwood, J., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. Trends Ecol. Evol. 20, 223–228.

Mabiletsa, P., 2004. Republic of south Africa, Tree Nuts Annual Report, Global Agriculture Information Network (GAIN). USDA Foreign Agricultural Service, pp. 1–7.

Mack, R.N., 1996. Predicting the identity and fate of plant invaders: emergent and emerging approaches. Biol. Conserv. 78, 107–121.

Matthew, K.M., 1999. The Flora of the Palini Hills, South India; Part two: Gamopetalae and Monochlamydeae. The Rapinat Herbarium, Tiruchirapalli, India.

Moodley, D., Geerts, S., Richardson, D.M., Wilson, J.R.U., 2013. Different traits determine introduction, naturalization and invasion success in woody plants: proteaceae as a test case. PLoS One 8, e75078.

Mucina, L., Rutherford, M.C., 2006. The vegetation of South Africa, Lesotho and Swaziland, Strelitzia. South African National Biodiversity Institute, Pretoria.

Myerscough, P.J., Whelan, R.J., Bradstock, R.A., 2001. Ecology of Proteaceae with special reference to the Sydney region. Cunninghamia 6, 951–1015.

Nagao, M.A., 2011. Farm and forestry production and marketing profile for Macadamia nut (*Macadamia integrifolia* and *M. tetraphylla*). In: Elevitch, C.R. (Ed.), Specialty Crops for Pacific Island Agroforestry. Permanent Agriculture Resources, Hōlualoa, Hawai'i.

Nel, J.L., Richardson, D.M., Rouget, M., Mgidi, T., Mdzeke, N., Le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L., Neser, S., 2004. A proposed

classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. South Afr. J. Sci. 100, 53–64.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34, 102–117.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.

Pyšek, P., Krivánek, M., Jarošík, V., 2009. Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90, 2734–2744.

Pyšek, P., Richardson, D.M., 2007. Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig, W. (Ed.), Biological Invasions. Springer, Berlin, pp. 97–125.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M., Kirschner, J., 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53, 131–143.

R Development Core Team, 2009. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Randall, R.P., 2007. The Introduced Flora of Australia and Its Weed Status. CRC for Australian Weed Management.

Rebelo, A.G., 1991–2001. The Protea Atlas Project. South African National Biodiversity Institute, Kirstenbosch.

Reichard, S.H., Hamilton, M.A., 1997. Predicting invasions of woody plants introduced into North America. Conserv. Biol. 11, 193–203.

Rejmánek, M., Richardson, D., 1996. What attributes make some plant species more invasive? Ecology 77, 1655–1661.

Rejmánek, M., Richardson, D.M., 2013. Trees and shrubs as invasive alien species – 2013 update of the global database. Divers. Distrib. 19, 1093–1094.

Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J., Grotkopp, E., 2005a. Ecology of invasive plants: state of the art. In: Mooney, H.A., Mack, R.M., McNeely, J.A., Neville, L., Schei, P., Waage, J. (Eds.), Invasive Alien Species: a New Synthesis. Island Press, Washington, DC, pp. 104–161.

Rejmánek, M., Richardson, D.M., Pyšek, P., 2005b. Plant invasions and invasibility of plant communities. In: van der Maarel, E. (Ed.), Vegetation Ecology. Blackwell Publishing, Oxford, pp. 332–355.

Richardson, D.M., Pyšek, P., 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog. Phys. Geogr. 30, 409–431.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M., Panetta, F., West, C., 2000. Naturalization and invasion of alien plants: concepts and definitions. Divers. Distrib. 6, 93–107.

Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species – a global review. Divers. Distrib. 17, 788–809.

Richardson, D.M., Carruthers, J., Hui, C., Impson, F.A.C., Miller, J.T., Robertson, M.P., Rouget, M., Le Roux, J.J., Wilson, J.R.U., 2011. Human-mediated introductions of Australian acacias – a global experiment in biogeography. Divers. Distrib. 17, 771–787.

Richardson, D.M., Pyšek, P., 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. New. Phytol. 196, 383–396.

Richardson, D.M., Thuiller, W., 2007. Home away from home-objective mapping of high-risk source areas for plant introductions. Divers. Distrib., 299–312.

Richardson, D.M., Van Wilgen, B.W., Mitchell, D.T., 1987. Aspects of the reproductive ecology of four Australian Hakea species (Proteaceae) in South Africa. Oecologia 71, 345–354.

Rodríguez-Castañeda, G., Hof, A.R., Jansson, R., Harding, L.E., 2012. Predicting the fate of biodiversity using species' distribution models: enhancing model comparability and repeatability. PLoS One 7, e44402.

Rouget, M., Richardson, D.M., 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. Am. Nat. 162, 713–724.

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

Sedgley, M., Criley, R.A., Coetzee, J.H., Littlejohn, G.M., Ben-Jaacov, J., Silber, A., 2007. Proteaceous ornamentals: Banksia, Leucadendron, Leucospermum, and Protea. In: Janick, J. (Ed.), Scripta Horticulturae. International Society for Horticultural Science, Belgium.

Simberloff, D., 2009. The role of propagule pressure in biological invasions. Annu. Rev. Ecol. Evol. Syst. 40, 81–102.

Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. Science 240, 1285–1293.

Tutin, T.G., 1993. Psilotaceae to Platanaceae, second ed. Cambridge University Press, Cambridge, UK.

VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E., 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecol. Model. 220, 589–594.

Vilà, M., Ibáñez, I., 2011. Plant invasions in the landscape. Landsc. Ecol. 26, 461–472.

Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol. Appl. 21, 335–342.

Webber, B.L., Yates, C.J., Le Maitre, D.C., Scott, J.K., Kriticos, D.J., Ota, N., McNeill, A., Le Roux, J.J., Midgley, G.F., 2011. Modelling horses for novel climate courses: insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. Divers. Distrib. 17, 978–1000.

Williams, P.A., 1992. *Hakea salicifolia*: biology and role in succession in Abel Tasman National Park, New Zealand. J. R. Soc. N. Z. 22, 1–18.

Williamson, M.H., Brown, K.C., 1986. The analysis and modelling of British invasions. Phil. Trans. R. Soc. B 314, 505–522.

Wilson, J.R.U., Ivey, P., Manyama, P., Nänni, I., 2013. A new national unit for invasive species detection, assessment and eradication planning. South Afr. J. Sci. 109, 1–13.

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

Zengeya, T.A., Robertson, M.P., Booth, A.J., Chimimba, C.T., 2013. Ecological niche modeling of the invasive potential of Nile tilapia *Oreochromis niloticus* in African river systems: concerns and implications for the conservation of indigenous congenerics. Biol. Invas. 15, 1507–1521.

Table S1. The performance of ten replicate models developed for *Hakea salicifolia* in the native range. Correctly predicted presence and absence data were evaluated using the area under the receiver operating characteristic curve (AUC).The standards for these indicators are also specified.

Model replicate	AUC
1	0.983
2	0.992
3	0.986
4	0.990
5	0.983
6	0.989
7	0.987
8	0.990
9	0.987
10	0.978
Mean	0.987

Accuracy indicator	AUC values (Swets, 1988)
Fail	0.50 - 0.60
Poor	0.60 - 0.70
Fair	0.70 - 0.80
Good	0.80 - 0.90
Excellent	> 0.90

Table S2. Contribution of each bioclimatic variable predicted from the model.

Variable	Percentage contribution
Precipitation of the driest quarter (Bio 17)	71.9
Precipitation of the wettest quarter (Bio 16)	15.5
Maximum temperature of the warmest month (Bio 5)	7.6
Mean temperature of the coldest quarter (Bio 11)	5.1

Table S3. Linear regressions of the factors influencing naturalization of *Hakea salicifolia* populations in South Africa, using single predictor models. (A) All surveyed populations (n=62); (B) populations in areas with suitable climatic conditions (n=54). Median and range of the data are given for continuous variables.

(A)

Variable	Summary (median, range)	Test	Relationship
Elevation	329, 42 - 1472	$z = -1.785$, $P = 0.0743$	No effect
Stem diameter	14, 4.10 - 30	$z = 1.205$, $P = 0.228$	No effect
Number of planted individuals (log transformed)	68, 1-1530	$z = 0.632$, $P = 0.528$	No effect
Seed output (log transformed)	144000, 0 - 13040000	$z = 2.311$, $P = 0.0209$	Populations with greater number of seeds are more likely to naturalize
Height (log transformed)	544.5, 210 - 1075	$z = -0.200$, $P = 0.842$	No effect
Habitation		$z = -0.699$, $P = 0.484$	No effect
Natural vegetation		$z = -0.430$, $P = 0.667$	No effect
Orchard		$z = -0.128$, $P = 0.898$	No effect
Pastoral land		$z = -0.982$, $P = 0.326$	No effect
Plantation		$z = 1.610$, $P = 0.107$	No effect
Rail/Road		$z = 1.212$, $P = 0.226$	No effect
Transformed		$z = 1.610$, $P = 0.107$	No effect
Vacant land		$z = -0.430$, $P= 0.667$	No effect
Management		$z = -0.922$, $P = 0.356$	No effect
Forest		$z = 0.007$, $P = 0.994$	No effect
Fynbos		$z = -0.007$, $P = 0.995$	No effect
Grassland		$z = -0.007$, $P = 0.994$	No effect
Savanna		$z = -0.011$, $P = 0.991$	No effect
Soil pH	7, 5 - 8	$z = 0.397$, $P = 0.691$	No effect
Soil drainage		$z = 1.760$, $P = 0.0784$	No effect

(B)

Variable	Summary (median, range)	Test	Relationship
Elevation	295.5, 42 -1472	$z = -1.858, P = 0.0631$	No effect
Stem diameter	14, 4.10 - 30	$z = 0.909, P = 0.364$	No effect
Number of planted individuals (log transformed)	68, 1 - 917	$z = 0.013, P = 0.989$	No effect
Seed output (log transformed)	144000, 0 - 13040000	$z = 2.110, P = 0.034$	Populations with greater number of seeds are more likely to naturalize
Height (log transformed)	550, 210 - 1075	$z = -0.942, P = 0.346$	No effect
Habitation		$z = 0.000, P = 1.000$	No effect
Natural vegetation		$z = 0.000, P = 1.000$	No effect
Orchard		$z = 0.000, P = 1.000$	No effect
Pastoral land		$z = -1.178, P = 0.239$	No effect
Plantation		$z = 1.001, P = 0.317$	No effect
Rail/Road		$z = 0.679, P = 0.497$	No effect
Transformed		$z = 1.178, P = 0.239$	No effect
Vacant land		$z = -0.777, P = 0.437$	No effect
Management		$z = -0.310, P = 0.756$	No effect
Forest		$z = 0.007, P = 0.994$	No effect
Fynbos		$z = -0.007, P = 0.995$	No effect
Grassland		$z = -0.007, P = 0.994$	No effect
Savanna		$z = -0.011, P = 0.991$	No effect
Soil pH	7, 5 - 8	$z = 1.045, P = 0.296$	No effect
Soil drainage		$z = 1.655, P = 0.098$	No effect

Table S4. The role of propagule pressure in driving naturalization of *Hakea salicifolia* in climatically suitable (n=26) and unsuitable (n=36) areas, tested in a generalized linear model.

Coefficients	Estimate	Standard error	*z* value	Pr (>|z|)
Intercept	-2.70	1.82	-1.48	0.14
log(seed output + 1)	0.21	0.14	1.41	0.16
Suitability	-2.22	3.37	-0.66	0.50
log(seed output + 1) : Suitability	0.29	0.30	0.98	0.32

Figure S1. Pair-wise plots between the predictor variables. Predictors with correlated variables (Kendall rank correlation coefficient > 0.65) were removed from the model. The correlation coefficients increase in size as the correlation between the predictors increase. NA values indicate predictors that could not be analysed due to many missing data.
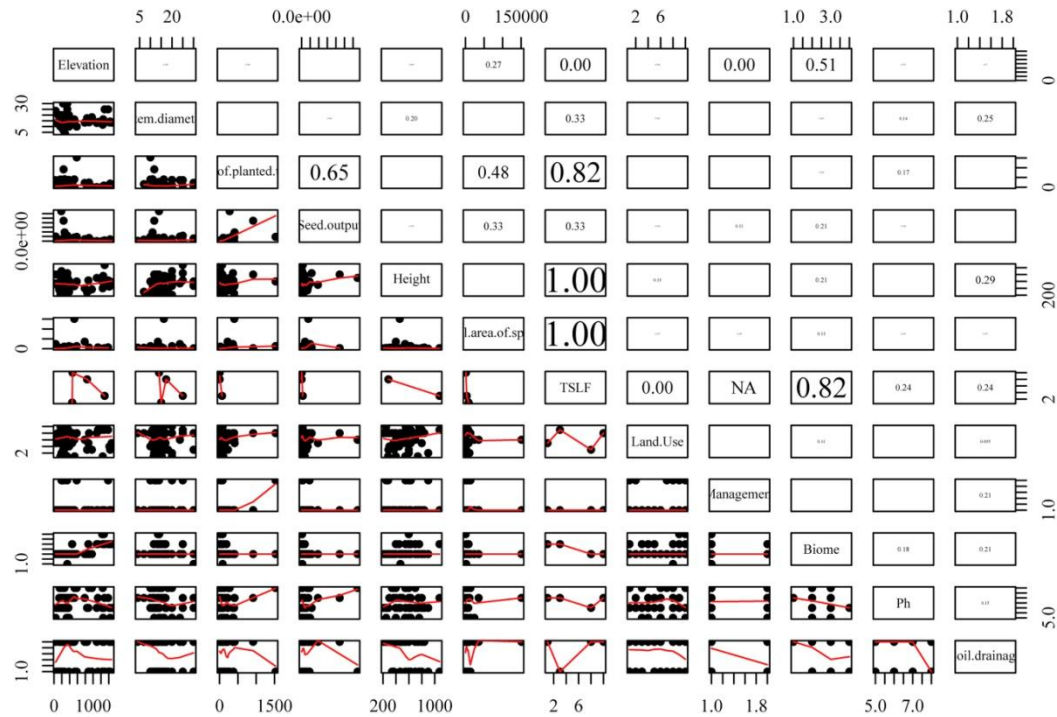
Figure S2. Marginal response curves which show the response of each variable in the multi-variate model when all other variables are set to their mean values: (a) precipitation of the driest quarter (b) precipitation of the wettest quarter (c) maximum temperature of the warmest month (d) mean temperature of the coldest quarter. The response curves depict the average of 10 replicate MaxEnt runs (red) and the mean of the standard deviations (dark blue).
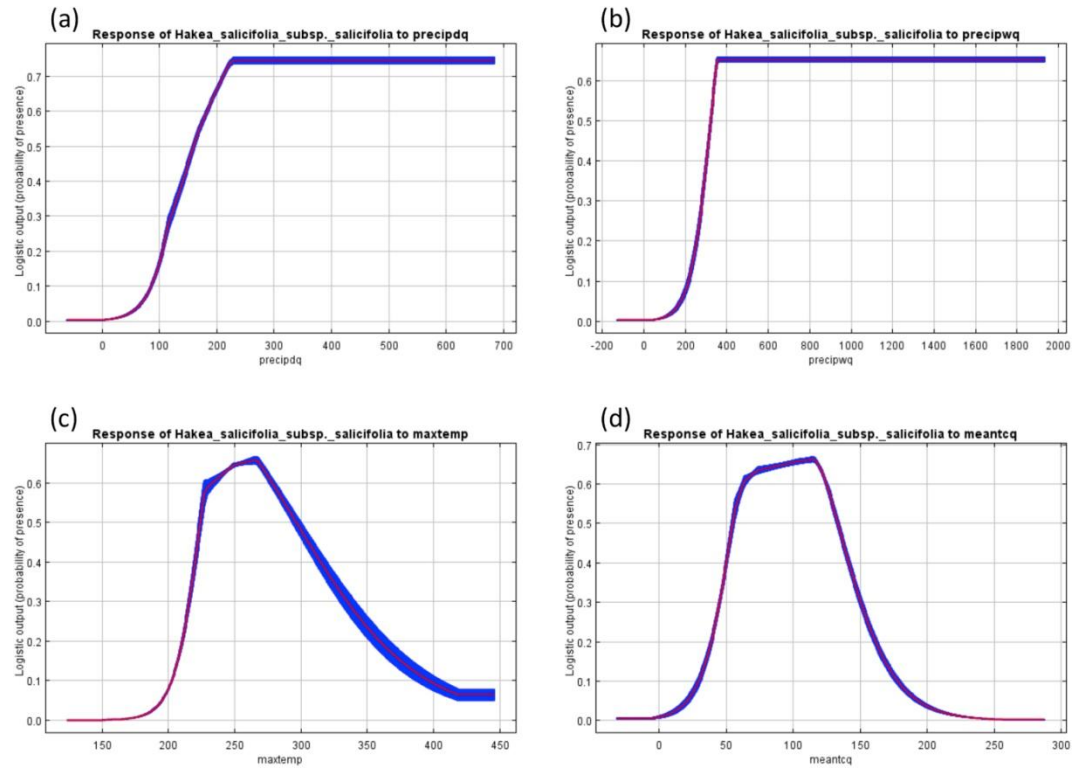
Figure S3. The major land use types of all naturalized and non-naturalized *Hakea salicifolia* populations. Habitation refers to populations planted in farm yards and gardens, transformed land is dominated by invasive alien plants and vacant land includes areas of open space which was abandoned.