



# Forestry trial data can be used to evaluate climate-based species distribution models in predicting tree invasions

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#### **Abstract**

Climate is frequently used to predict the outcome of species introductions based on the results from species distribution models (SDMs). However, despite the widespread use of SDMs for pre- and post-border risk assessments, data that can be used to validate predictions is often not available until after an invasion has occurred. Here we explore the potential for using historical forestry trials to assess the performance of climate-based SDMs. SDMs were parameterized based on the native range distribution of 36 Australian acacias, and predictions were compared against both the results of 150 years of government forestry trials, and current invasive distribution in southern Africa using true skill statistic, sensitivity and specificity. Classification tree analysis was used to evaluate why some Australian acacias failed in trials while others were successful. Predicted suitability was significantly related to the invaded range (sensitivity = 0.87) and success in forestry trials (sensitivity = 0.80), but forestry trial failures were under-predicted (specificity = 0.35). Notably, for forestry trials, the success in trials was greater for species invasive somewhere in the world. SDM predictions also indicate a considerable invasion potential of eight species that are currently naturalized but not yet widespread. Forestry trial data clearly provides a useful additional source of data to validate and refine SDMs in the context of risk assessment. Our study identified the climatic factors required for successful invasion of acacias, and accentuates the importance of integration of status elsewhere for risk assessment.

#### **Keywords**

Species distribution models, model evaluation, Australian acacias, classification tree, forestry, alien trees, invasions, Southern African Plant Invaders Atlas

#### Introduction

Predicting which species will escape from forestry plantations and become invasive remains a challenge in invasion biology (Daehler et al. 2004). Such prediction is an essential requirement for proactive management (Ficetola et al. 2007). Propagule pressure, residence time, species traits, environmental factors, interactions of introduced species with the native species, and historical factors have all been indicated as drivers of invasion success (Castro-Díez et al. 2011; Křivánek et al. 2006; Lockwood et al. 2009; Pyšek et al. 2009; Thuiller et al. 2006; Wilson et al. 2007), with invasions from silviculture as no exception (Castro-Díez et al. 2011; Gallagher et al. 2011). However, climate plays a fundamental role in determining species distributions (Gaston 2003), and the predictive success of invasive risk assessments is still largely a function of invasiveness elsewhere and climate suitability (Hulme 2012).

Species distribution models (SDMs) have been widely used to predict invasions (Elith and Leathwick 2009; Pauchard et al. 2004; Peterson 2003; Zhu et al. 2007). An SDM is a mathematical description of the species distribution in environmental space that can be used to predict the distribution of species in geographic space (Peterson et al. 1999). The models combine species occurrence records and environmental variables (Peterson and Holt 2003) to create a climatic envelope model. The resulting model can be projected to any geographic space to identify regions that are suitable for species. The models can be based on native distribution records, introduced distribution records, or both (Steiner et al. 2008). SDMs can therefore be used to identify areas that are suitable for species even before introduction to predict which areas are likely to be invaded (Guisan and Zimmermann 2000). SDMs have considerable potential in risk assessment but they are seldom tested in predicting successful tree establishments but see Nuñez and Medley (2011).

The use of SDMs in management of invasive species can be considerably improved by independent datasets to validate SDM predictions (Allouche et al. 2006; Fielding and Bell 1997). Appropriate datasets should contain information on species that were repeatedly introduced in different localities with a clear indication of introduction outcome (i.e. success or failure). It is important that the records on introduction outcome explicitly indicate which factors influenced the outcome (e.g. climate or biotic). However, these ideal datasets are rarely available. Therefore, invaded range data have been used to evaluate SDM predictions (McGregor et al. 2012b; Nuñez and Medley 2011; Nel et al. 2004; Rouget et al. 2004; Wilson et al. 2007). However, such analyses are limited to established widespread invasive species, ignoring any failed introductions.

While alien trees and shrubs have been introduced in different parts of the world to fulfil a wide range of human needs (Richardson and Rejmánek 2011), historically forestry has been one of the most important pathways (Pyšek et al. 2009; 2011). In-

troduced forestry species contribute to the economies of many countries, but can also cause major problems as invaders of natural and semi-natural ecosystems (Essl et al. 2010, 2011; Richardson and Rejmánek 2011). Such introductions have often been well documented, for example government forestry trials throughout southern Africa were reviewed by (Poynton 1979a, b; 2009). The data from these trials provide historical information on intentional introductions and on their outcome, making it possible to explore factors influencing the success of introductions across different areas.

The aims of this study are to evaluate species distribution models using both forestry trial data and invaded range data, and to investigate why some trials succeeded while others failed. To do this, we narrowed the taxonomic range to a well studied group, Australian acacias. Australian acacias are a good model group to understand plant invasions because *Acacia* is a speciose genus that contains many introduced and invasive species (Richardson et al. 2011). They are also a good group for exploring SDMs because native ranges in Australia and introduced ranges in southern Africa are well known and documented (Van Wilgen et al. 2011). Around 80 Australian acacias have been introduced in southern Africa, 36 of which were included in forestry trials (Richardson et al. 2011; Poynton 2009, Table 1). Currently, sixteen *Acacia* species are confirmed as invasive and three species are reported to be naturalized, but it is not clear whether other species are also likely to invade or not (Richardson et al. 2010, 2011; Van Wilgen et al. 2011; Wilson et al. 2011).

First we used data on the outcome of forestry trials and data on invasive plant distributions to evaluate SDMs. We then assessed why some forestry trials succeeded but others failed. Lastly, we determine which introduced species have a large potentially suitable but not currently occupied range, i.e. which species have a high invasion debt (Essl et al. 2011).

#### **Methods**

### Study species and datasets

Species distribution models for Australian acacias were calibrated using occurrence records from their native range (Australia) and then projected to southern Africa based on Richardson et al. (2011) approach. The models were evaluated using presence records from the invaded range in the Southern African Plant Invaders Atlas (SAPIA: Henderson 2007) and records of success and failure obtained from government forestry trials (Poynton 2009).

## Species distribution modelling

#### Model calibration

Numerous approaches have been developed to model the potential distribution of invasive species with various degrees of success (Gallien et al. 2012; Peterson 2003).

Here we chose a simple SDM approach that was quick to implement. The models were originally developed for 838 Australian *Acacia* species (Richardson et al. 2011). The approach was slightly modified as our pilot study indicated that some of the species ranges were under-predicted when using the exact approach. Minimum and maximum values for each variable over the range of species occurrence were used to define the range of each species. We also decided to use four predictor variables instead of six as this gave more sensible predictions. The model that we produced is equivalent to the marginal range of BIOCLIM but uses only four predictor variables (Nix 1986).

We obtained a dataset of occurrence records for the selected species (Table 1) from the Australian Virtual Herbarium (accessed 29<sup>th</sup> June 2010) with only one occurrence record retained per 10 minute grid cell for each species to reduce spatial sampling bias. Richardson et al. (2011) reported that to clean data all names were checked against the native species list while hybrid, varieties, subspecific information and authorities were generally removed for simplicity and to make the list comparable. The four bioclimatic variables used to build the SDMs were annual mean temperature (Bio\_1), maximum temperature of the warmest month (Bio\_5), minimum temperature of coldest month (Bio\_6), and annual precipitation (Bio\_12) all obtained at a 10 minute spatial resolution from Worldclim [www.worldclim.com (Hijmans et al. 2005)].

For each species we calculated the minimum and maximum values extracted from occurrence records for each predictor variable. These values were used to identify the range of values that each species could tolerate. For each species, we reclassified each of the four predictor variable maps into a map consisting of presence (value = 1) or absence (value = 0), using the minimum and maximum values calculated for that species. We then multiplied these presence/absence maps to generate a final map indicating the potential distribution of that species. The analysis was conducted using the R statistical software (v. 2.11, R Development Core Team 2010). The models were projected to southern Africa to identify climatically suitable regions for each species.

#### Model evaluation

We evaluated the relationship between predicted distributions and actual distributions (forestry trials and SAPIA data) using several measures. Sensitivity is the proportion of observed presences predicted present and quantifies the omission error; specificity is the proportion of observed absences predicted absent and quantifies commission error (Fielding and Bell 1997). These measures range from 0 to 1 with 0 indicating no agreement between predicted and actual data and 1 indicating a perfect agreement. True skill statistic (TSS) includes omission and commission errors (Allouche et al. 2006; Fielding and Bell 1997), and ranges from -1 to +1, where +1 indicates perfect agreement and values of zero or less indicates a performance no better than random. We used TSS to evaluate SDMs because TSS has been shown to be insensitive to prevalence (Allouche et al. 2006).

**Table 1.** The number of government forestry trials, the number of successful trials; the number of records in SAPIA, the number of QDGCs occupied in South Africa, Lesotho and Swaziland; and status in southern Africa for the species explored in the study.

Species	Total number of trials	Success	Number of records in SAPIA	QDGCs occupied in SA	Status in southern Africa	
A. acuminata	13	3	0	0	Introduced	
A. adunca	1	0	2 2		Naturalized	
A. adsurgens	2	2	0	0	Introduced	
A. aneura	4	3	0 0		Introduced	
A. aulacorpa	4	2	0	0 0		
A. auriculiformis	3	2	0	0	Introduced	
A. baileyana	5	4	184	101	Invasive	
A. binervata	1	1	0	0	Introduced	
A. cowleana	2	1	0	0	Introduced	
A. crassicarpa	2	1	0	0	Introduced	
A. cultriformis	7	3	1	1	Naturalized	
A. cyclops	2	2	1282	172	Invasive	
A. dealbata	13	12	1667	299	Invasive	
A. decurrens	5	2	341	124	Invasive	
A. elata	9	3	99	48	Invasive	
A. falciformis	4	2	0	0	Introduced	
A. fimbriata	1	1	1	1	Naturalized	
A. holosericea	4	1	1	0	Introduced	
A. implexa	0	0	3	3	Invasive	
A. leptocarpa	2	2	0	0	Introduced	
A. ligulata	1	1	0	0	Introduced	
A. longifolia	5	4	446	97	Invasive	
A. mangium	3	1	0	0	Introduced	
A. mearnsii	13	10	4313	462	Invasive	
A. melanoxylon	28	20	678	167	Invasive	
A. paradoxa	1	1	4	2	Invasive	
A. pendula	6	3	0	0	Introduced	
A. podalyriifolia	3	2	159	78	Invasive	
A. prominens	2	2	0	0	Introduced	
A. pycnantha	9	8	182	38	Invasive	
A. retinodes	2	2	0	0 0		
A. rubida	1	1	0 0		Introduced	
A. saligna	8	5	1302	164	Invasive	
A. schinoides	1	1	0	0	Introduced	
A. stricta	0	0	6	6	Invasive	
A. viscidula	1	1	1	1	Naturalized	
Total	168	109	10672	1766		

## The role of forestry trials and invaded range data for SDMs evaluation Government forestry trials

In southern Africa, forestry trials for Australian acacias were conducted at 67 stations from the 1820s to the 1960s for 36 species (Poynton 2009). Trial data include records on introduction date (that can be used to quantify the importance of residence time in explaining invasions), and the number of stations and the number of times that a species was trialled (that can be used to quantify the effect of propagule pressure). The forestry trials dataset covers ten countries (namely, Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia, and Zimbabwe), i.e. most of southern Africa.

Of the 168 forestry trial records obtained from this dataset, 129 records had precise geographic location and trial outcome and could be used to evaluate the SDMs (see Table 1). While subspecific taxa can occupy different climatic niches (Thompson et al. 2011), for simplicity and as naming was not consistent or verifiable, all species that had varieties or subspecies were grouped together (e.g. plantings of *Acacia longifolia* subsp. *longifolia* and *Acacia longifolia* ssp. *sophorae* were considered jointly as *Acacia longifolia*). We also only analysed species with four or more trials. This gave 14 Australian acacias with which to evaluate SDMs and the relative importance of variables in explaining the outcome of the forestry trials. We quantified the accuracy of predictive power of SDMs for each species (n=14) found in forestry trials by calculating true skill statistic, sensitivity and specificity.

## Southern African Plant Invaders Atlas (SAPIA)

This dataset contains records for over 700 naturalized and invasive species, with information on abundance, habitat preferences, time of introduction and distribution (Henderson 1998). Here we restricted our analyses to Lesotho, South Africa and Swaziland as the other regions are relatively poorly sampled and use the SAPIA version accessed April 2012. The accuracy of SDMs for each species (n=11) found in SAPIA was quantified by calculating sensitivity only as SAPIA is a presence only dataset.

## Why did some forestry trials succeed while others failed?

A classification tree approach (Breiman et al. 1984) was used to identify which of several potential predictor variables could predict the outcome of forestry trials (Table 2). We considered the following variables: 1) indication of herbivory or other biotic factors (birds or hares eating seedlings as noted on the original trial record); 2) climatic suitability; 3) South African Biome; and 4) the invasive status of the species globally. The current invasive status in South Africa and global invasive status of each species

Variable	Coded	Criteria	Justification	Data sources
Trial outcome	0/1	0- failure (absence) 1-success (presence)		Poynton (2009)
Biotic	Y/N	Did species fail because seeds were eaten by animals and birds?	Biotic factors have been indicated to influence survival that can lead to naturalization (Nuñez and Medley 2011)	Poynton (2009)
Climatic suitability	0/1	0-Climate not suitable 1-Climate suitable	Climatic suitability is widely used to predict outcome of introductions McGregor et al. (2012).	Species distribution models
Climatic variables	Bio_1,bio_5, bio_6, bio_12	Annual Mean temperature, Maximum Temperature of the Warmest Month, Minimum Temperature of the Coldest Month & Annual precipitation	Did trials succeed because of precipitation and temperature ranges? Castro-Díez et al. (2011)	Hijmans et al. (2006)
Biome	Names	South African biomes	Were trials successful because of the biomes they were introduced to? Rouget et al. (2004)	Mucina and Rutherford (2006)
Status	Introduced, Natura- lized or invasive (sensu Richardson et al. 2000)	Invasiveness elsewhere according to Richardson et al. (2011)	Invasiveness elsewhere is one of the best predictors of the outcome of species introductions Hulme (2012)	Richardson et al. (2011)

**Table 2.** Variables used to quantify why some forestry trials of *Acacia* species in southern Africa succeeded while others failed.

were obtained from Richardson et al. (2011). Climatic suitability was coded as either suitable or unsuitable as predicted by SDMs and biotic factors [e.g. whether seeds or seedlings were eaten by hares or birds as recorded in Poynton (2009)] were coded as either yes or no depending on trial outcome.

The classification tree was constructed by repeatedly splitting data, defined by a simple rule based on a single explanatory variable at each split. At each split, the data were partitioned into two exclusive groups, each of which was as homogeneous as possible (Breiman et al. 1984). An optimal tree was then determined by testing for misclassification error rates for the largest tree as well as for every smaller tree by tenfold cross-validation constructed in CART Pro Ex v. 6.0. The program builds a nested sequence of branches by recursively snipping off the less important splits in terms of explained deviance. The length of the tree was controlled by choosing the one-SE rule, which minimizes cross-validated error within one standard error of the minimum cost tree rule (Pyšek et al. 2009).

## Which species that are not yet widespread have a large potential suitable range?

Occupancy of each species was calculated at the quarter degree grid cell (QDGC, 15 min. × 15 min.) level. The current distribution of Australian acacias in Lesotho, South

Africa, and Swaziland was based on the number of QDGCs occupied as recorded in both the SAPIA and the forestry trial databases. Species potential distribution was estimated based on climatic suitability and range size as the percentage of southern Africa (South Africa, Lesotho and Swaziland) predicted suitable by SDMs.

### Results

## Evaluation of SDMs using forestry trials and invaded range data

The SDMs successfully predicted the outcome (success or failure) for 81 of the 129 forestry trials (63%) (overall TSS = 0.15, Table 3), with a high percentage of true presences predicted as present (sensitivity = 0.80) but a rather low percentage of true absences predicted as absent (specificity = 0.35). However, there was a higher proportion of false absences than false presences (Table 3). SDM evaluation varied between species, with five species having low sensitivity values and ten with low specificity values (Table 3).

Observed invasive ranges of Australian acacias in southern Africa are generally correctly predicted as suitable based on the SDMs (sensitivity = 0.87). However, the predictions mismatched 461 (13%) invasive range records (i.e. 13% of the records indicate that species invaded areas that are climatically unsuitable; Table 4). Most of the invasive species have the potential to substantially increase their ranges because more than half of southern Africa is predicted to be suitable.

Acacia dealbata and A. mearnsii are provided as visual examples (Fig. 1).

## Explaining success or failure of forestry trials

Using climatic suitability alone, 81 trials out of 129 (model accuracy = 0.63) were correctly predicted (Table 3), while 87 (model accuracy = 0.67) records were correctly predicted by the criterion "invasive elsewhere" (Fig. 2: Node 2 and 3). Based on the classification tree (Fig. 2), three variables (invasive elsewhere, annual mean temperature, and mean temperature of the coldest month) together accurately predicted 72% of the forestry trial records (i.e. 93 trials). The classification tree analysis correctly predicted forestry trial outcome significantly (sensitivity = 086, specificity = 0.36 and TSS = 0.22).

## Determining species that have a high risk of becoming widespread invaders

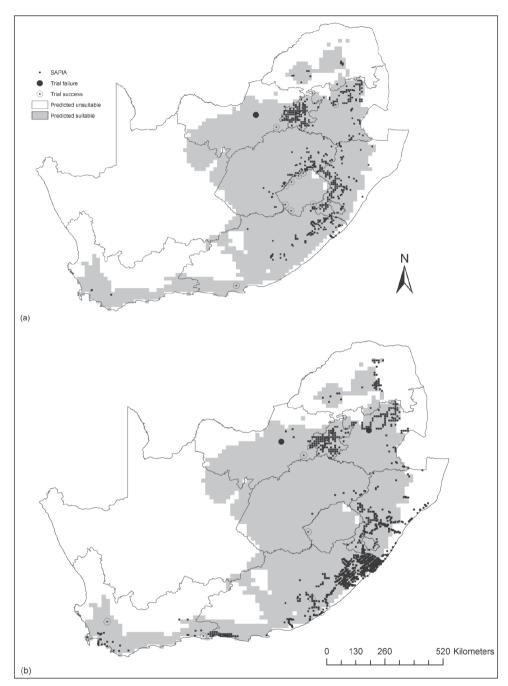
The wetter parts of the region were identified as most suitable for the analysed suite of Australian acacias. SDMs predicted that thirteen species can be widespread with 20 % of southern Africa predicted to be suitable [Acacia acuminata, A. adunca, A. aneura,

**Table 3.** Measures used to evaluate models using government forestry trials dataset in southern Africa; a-number of cells for which presence was correctly predicted by the model; b- number of cells for which the species was not found but the model predicted presence; c, number of cells for which the species was found and the model predicted absence; d, number of cells for which absence was correctly predicted by the model. Sensitivity (proportion of actual presences predicted as such); specificity (proportion of actual absences predicted as such); TSS [true skill statistic (sensitivity + specificity-1].

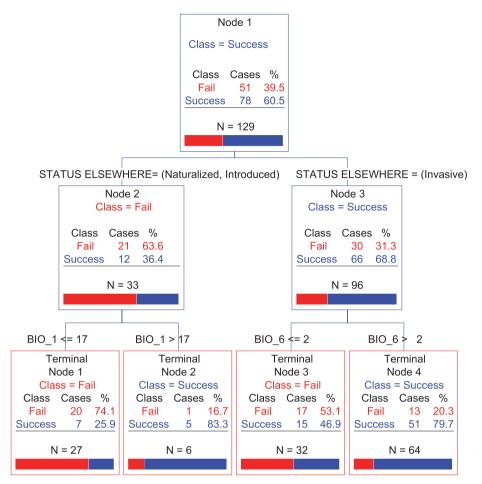
Species	Number of trials	a	Ь	С	d	Sensitivity	Specificity	TSS
A. acuminata	13	1	5	1	6	0.50	0.54	0.04
A. aneura	4	1	1	2	0	0.33	0.00	-0.67
A. baileyana	5	4	1	0	0	1.00	0.00	0.00
A. cultriformis	5	0	2	1	2	0.00	0.50	-0.50
A. dealbata	13	11	0	1	1	0.91	1.00	0.91
A. decurrens	7	2	4	0	1	1.00	0.20	0.20
A. elata	9	2	4	2	1	0.50	0.20	-0.30
A. falciformis	4	2	2	0	0	1.00	0.00	0.00
A. longifolia	5	4	1	0	0	1.00	0.00	0.00
A. mearnsii	13	7	2	3	1	0.70	0.33	0.03
A. melanoxylon	28	20	8	0	0	1.00	0.00	0.00
A. pendula	6	1	1	2	2	0.33	0.67	0.00
A. pycnantha	9	7	1	1	0	0.88	0.00	-0.20
A. saligna	8	2	0	3	3	0.40	1.00	0.40
Overall	129	64	32	16	17	0.80	0.35	0.15

**Table 4.** Measures used to evaluate models using Southern African Plant Invaders Atlas; a-number of cells for which presence was correctly predicted by the model; c-number of cells for which the species was found but the model predicted absence.

Species	Number of records	a	С	Sensitivity	
A. baileyana	86	82	4	0.95	
A. cyclops	141	137	4	0.97	
A. dealbata	717	707	10	0.99	
A. decurrens	157	155	2	0.99	
A. elata	20	17	3	0.85	
A. longifolia	79	79	0	1.00	
A. mearnsii	1916	1485	431	0.78	
A. melanoxylon	163	163	0	1.00	
A. podalyriifolia	56	51	5	0.91	
A. pycnantha	83	82	1	0.99	
A. saligna	53	52	1	0.98	
Overall	3471	3010	461	0.87	

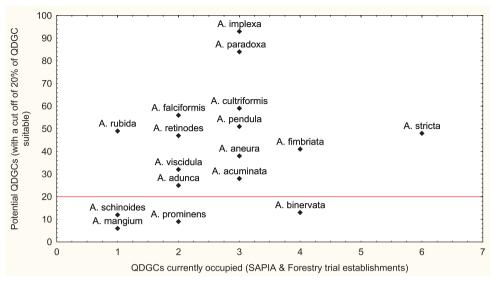


**Figure 1.** Current distribution [from both forestry trials (noted as trial failure or success) and SAPIA] and potential distribution for: **a** *Acacia dealbata* and **b** *A. mearnsii* in Lesotho, South Africa, and Swaziland.



**Figure 2.** Classification tree analysis of the probability that a species will succeed (blue part of the bar) or fail (red) in southern African forestry trials based on various variables (see Table 2: trial data and variables used). Each node shows the number of successes and failures in each class, the total number of cases (N) and a graphical presentation of the percentage of success and failure cases (horizontal bar). For each node the splitting criterion is written in caps on top of the nodes. Status is similar to invasiveness elsewhere and the two environmental variables: Bio\_1 is annual mean temperature and Bio\_6 is minimum temperature of the coldest month.

A. cultriformis, A. falciformis, A. fimbriata, A. implexa, A. paradoxa, A. pendula, A. retinodes, A. rubida, A. stricta, and A. viscidula (Fig. 3)]. The remaining four species (A. mangium, A. prominens, A. schinoides and A. binervata), appear to have a potential of localized extensive spread (Fig. 3). All of these species have not yet reached the full extent of climatically suitable ranges (see Appendix – Fig. S1).



**Figure 3.** The relationship between potential and current distributions in Lesotho, South Africa, and Swaziland expressed as total number of QDGCs currently occupied from SAPIA and forestry trial successes (with a cut off of 20% of southern Africa QDGCs climatically suitable) for 17 species that are not yet widespread in southern Africa.

### Discussion

In this study, we found that forestry trial data provided useful data for SDM evaluation as it contains information on species that were repeatedly introduced in different localities within southern Africa with a clear indication of trial outcome. Trials were successful in areas that are predicted as climatically suitable by SDMs (sensitivity = 0.80; Table 3). McGregor et al. (2012b) found that successful naturalization of pine species in plantations was linked to a good climate match between their native range and introduced ranges. The results emphasize the value of incorporating forestry data in to SDMs when predicting species distributions.

SDMs could not accurately predict the failures of species in trials (specificity = 0.35; Table 3) and this suggests that climatic suitability only provides a broad picture of where an introduced species might survive, but there are other factors that determine whether an introduced species will be successful like biotic interactions and evolutionary capacity to adapt (Blackburn et al. 2011; Nuñez and Medley 2011; Soberón and Peterson 2005). Factors such as seed predation, competition with local plants and herbivory can have strong effects on *Acacia* success in trials.

SDMs correctly identified invaded ranges of Australian acacias in southern Africa. SDMs correctly predict regions of introduction but not the total invaded ranges (e.g. *A. mearnsii*, Fig. 1). Similarly, previous studies indicated that SDMs calibrated on native range records were able to predict region of introduction, but not the total invaded range, indicating a possible niche shift (Beaumont et al. 2009; Broennimann et al.

2007). This suggests that species may alter climatic niches during the invasion process. However, there is an on-going debate in literature about the prevalence of niche shift (Peterson 2011). According to the SDMs predictions, even widespread species (e.g. *A. dealbata*) have not yet fully occupied all climatically suitable areas in southern Africa. So management actions should be focused on containment, with resources dedicated to detecting and removing outlying populations of such species.

In line with other studies, we found that the success of species after introduction in the new ranges was greater for species recorded as invasive elsewhere (McGregor et al. 2012a; Reichard and Hamilton 1997; Scott and Panetta 1993; Williamson and Fitter 1996). As such Australian acacias that succeeded in trials appear to be a non-random subset in the global pool: they tended to be species that are invasive elsewhere and are within climatic areas similar to their native ranges hence they are likely to invade large areas. Since Australian acacias that are known to be invasive elsewhere are already planted in southern Africa for forestry purposes (Richardson et al. 2011), their spread should be controlled.

Australian Acacia species that are not yet widespread are likely to spread to currently unoccupied climatically suitable ranges as SDMs predictions indicate that a large portion of Lesotho, South Africa and Swaziland is suitable for invasion by 13 of the 17 currently introduced or naturalized (Fig. 3). We believe this is a major invasion debt and not simply an over-prediction in the SDMs, because there is a strong correlation between extent of usage and invasive distributions for Australian acacias in South Africa (Wilson et al. 2011). The widespread invaders are those species that have been planted for forestry, dune stabilization or ornamental purposes. However, many other introduced species were only ever planted in forestry trials or arboreta. As such their currently restricted distribution is the result of low propagule pressure, but given opportunities and time, these species can and do spread (Kaplan et al. 2012; Zenni et al. 2009; Kaplan et al. in press). Species that have a large potential range and are invasive elsewhere (Fig. 3 and Supplementary material Fig. S1) should be prioritised for management, and where possible eradicated, e.g. Acacia implexa, A. paradoxa and A. stricta in South Africa (Kaplan et al. 2012; Zenni et al. 2009; Kaplan et al. in press). Commercial forestry is one of the major pathways to tree invasions and availability of introduction data can be useful for screening potential invaders when coupled to SDMs. SDMs provide useful information that can influence management decisions on early detection, prioritization, and more targeted research. SDMs also provide information for rapid assessment of potential distributions of alien species based on climate, even before introduction.

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## **Appendix**

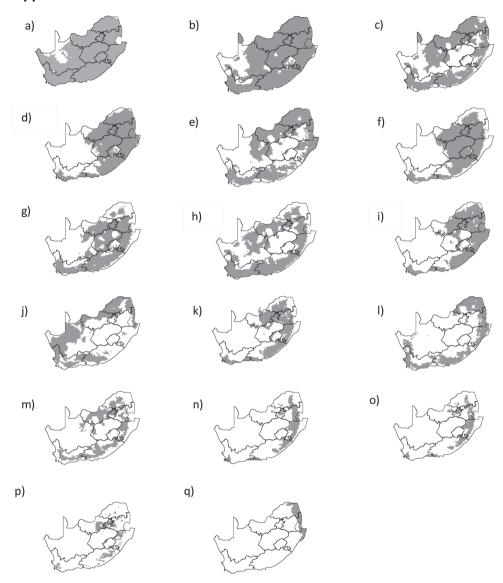


Figure S1. Current and potential distributions of sixteen species that are not widespread in southern Africa arranged on the basis of their suitable range size: a Acacia paradoxa b A. implexa c A. cultriformis d A. falciformis e A. pendula f A. rubida g A. stricta h A. retinodes i A. fimbriata j A. aneura k A. viscidula l A. acuminata m A. adunca n A. binervata o A. schinoides p A. prominens q A. mangium. The grey shading indicates areas that SDMs have identified as suitable by SDMs while the white shading indicates unsuitable areas.