Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale

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Abstract

Predicting the probability of successful establishment of plant species by matching climatic variables has considerable potential for incorporation in early warning systems for the management of biological invasions. We select South Africa as a model source area of invasions worldwide because it is an important exporter of plant species to other parts of the world because of the huge international demand for indigenous flora from this biodiversity hotspot. We first mapped the five ecoregions that occur both in South Africa and other parts of the world, but the very coarse definition of the ecoregions led to unreliable results in terms of predicting invasible areas. We then determined the bioclimatic features of South Africa's major terrestrial biomes and projected the potential distribution of analogous areas throughout the world. This approach is much more powerful, but depends strongly on how particular biomes are defined in donor countries. Finally, we developed bioclimatic niche models for 96 plant taxa (species and subspecies) endemic to South Africa and invasive elsewhere, and projected these globally after successfully evaluating model projections specifically for three well-known invasive species (*Carpobrotus edulis*, *Senecio glastifolius*, *Vellereophyton dealbatum*) in different target areas. Cumulative probabilities of climatic suitability show that high-risk regions are spatially limited globally but that these closely match hotspots of plant biodiversity. These probabilities are significantly correlated with the number of recorded invasive species from South Africa in natural areas, emphasizing the pivotal role of climate in defining invasion potential. Accounting for potential transfer vectors (trade and tourism) significantly adds to the explanatory power of climate suitability as an index of invasibility.

The close match that we found between the climatic component of the ecological habitat suitability and the current pattern of occurrence of South Africa alien species in other parts of the world is encouraging. If species' distribution data in the donor country are available, climatic niche modelling offers a powerful tool for efficient and unbiased first-step screening. Given that eradication of an established invasive species is extremely difficult and expensive, areas identified as potential new sites should be monitored and quarantine measures should be adopted.

Keywords: bioclimatic modelling, biological invasions, exotic species, invasive alien species, plant invasions, prediction, propagule pressure, risk assessment

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Introduction

The intentional or accidental movement of species by humans to regions far removed from their natural ranges has increased dramatically in frequency and extent in recent decades as human movements have become more global and international trade has increased (McNeely *et al.*, 2001; Levine & D'Antonio, 2003). Economic globalization thus, is, also reducing the regional distinctiveness of the Earth's biota (Sax & Gaines, 2003). Biological invasions affect human economic wealth by impacting on agriculture, forestry and health (Pimentel *et al.*, 2001), altering ecosystem functioning (Brooks *et al.*, 2004), and threatening native biodiversity (Mack *et al.*, 2000). Invasions are a significant component of human-mediated global environmental change (Vitousek *et al.*, 1997), which is altering the spatial distribution of physical conditions, habitats and species on Earth (Chapin *et al.*, 2000).

Once introduced species are established, they are difficult to eradicate (Rejmánek *et al.*, 2005). Preventing the introduction of potential invaders is by far the most cost-effective form of management. To this end, screening procedures have been developed in several parts of the world (Tucker & Richardson, 1995; Daehler *et al.*, 2004). Such systems for alien plants draw on a wide range of information, including whether a species is known to be invasive elsewhere, and various measures aimed at assessing the species' potential for dealing with features of the environment in question (Rejmánek *et al.*, 2005).

Similarity in climate between native and target regions has long been recognized as a basic requirement for a successful invasion (Panetta & Mitchell, 1991; Scott & Panetta, 1993). Establishment and spread of alien plants are sometimes limited by an imperfect climate match (Pyšek *et al.*, 2003). Several studies have tested the value of climate matching, or homoclime analysis, for assessing the risk of plant species from other regions of the world invading a given area (e.g. Curnutt, 2000). Although species diversity is co-determined by biophysical factors and, increasingly, land use, climate is the single most important driving factor at very broad continental and global scales (Woodward, 1987; Willis & Whittaker, 2002). By using a climate-based approach, scientific efforts can be focused on identifying species that pose the most serious threats as invaders in climatically similar regions.

Predicting the probability of successful establishment of plant species by matching climatic variables from native ranges to host ranges has a long history in silviculture (review in Mack, 1996) and continues to the present in many fields of ecology (Beerling *et al.*, 1995;

Zalba *et al.*, 2000; Peterson & Vieglais, 2001; Roura-Pascual *et al.*, 2004). The development of new fine-scale climatic data sets and powerful modelling tools (niche-based models) has improved the predictive power of these approaches (Guisan & Thuiller, 2005). Underpinning these studies is the assumption that species' climatic niches are likely to evolve only slowly and under circumscribed conditions (Holt, 1992), and that these represent a stable environmental constraint to their distribution (Peterson *et al.*, 1999). It follows that the present geographic distribution of a species can be projected using niche-based models that simulate the realized niche, into geographic dimensions that allow us to predict where the species will and will not be able to maintain populations (Guisan & Thuiller, 2005; Soberon & Peterson, 2005). Such models can accurately predict the overall range of a species including both the native and adventive distribution areas worldwide, and can also take into account potential future responses to global climate change (Roura-Pascual *et al.*, 2004).

The climate-matching approach has some limitations that can appear as both false positives and false negatives. The former occurs when environmental variables other than climate (such as soil type, disturbance regime, or interspecific interactions) preclude the naturalization of a species in a host area. False negatives occur if a species' potential distribution has not been realized in its native range because of nonequilibrium situation, historical constraints attributable to human influences or because of physical barriers that prevent full occupancy of an area by the species (Curnutt, 2000). Climate matching also ignores aspects of species life history such as fecundity and dispersal ability, both key components of potential invasion rate (Higgins & Richardson, 1999). For these reasons, niche-based modelling cannot provide perfect predictions of future invasions, but its major advantage (especially in the absence of viable alternatives) is that the invasion potential of large numbers of species can be assessed before introduction (Peterson & Vieglais, 2001).

Our study is novel in several aspects. First, most previous studies have focused on species-specific assessments of climate suitability and none has attempted multispecies projections to examine global risks of species invasions. Second, by adopting a source–area approach and evaluating the potential for species invasions from a particular region, important biases associated with varying chances of individual species for long-distance translocation by humans are reduced (Pyšek *et al.*, 2004). There are good reasons for selecting South Africa as a model source area of invasions worldwide. South Africa is not only severely impacted by alien invasive species (Richardson *et al.*, 2000a), but as a biodiversity hotspot, it serves as an important

donor of invasive species for other parts of the world (Pyšek, 2004). The increase in tourism to South Africa, the explosion of global trade and the huge demand for its flora from all over the world create the potential for an increasing number of South African plant species to sample potentially suitable habitats elsewhere.

In this paper, we present three different ways of identifying parts of the world that are potentially susceptible to invasion by plant species native to South Africa. First, we simply map the WWF Global 200 ecoregions (Olson *et al.*, 2001) occurring both in South Africa and other parts of the world. Second, we determine the bioclimatic features of South African vegetation biomes (Mucina & Rutherford, 2005) and project the potential distribution of analogous areas throughout the world. Third, we develop species' distribution models for 96 plant taxa endemic to South Africa and invasive elsewhere, and project these globally after evaluating model projections. This allows us to define the high-risk regions susceptible to invasion by South African flora.

Finally, we relate the number of species of South African origin reported to be invasive in other parts of the world (Weber, 2003) to the results of predictive climate-match modelling and quantify key transfer vectors, trade and tourism, to corroborate the importance of propagule pressure (Lonsdale, 1999).

Material and methods

Data sets

For the ecoregion mapping, we used the classification and mapping of ecoregions of Olson *et al.* (2001). Of 12 global ecoregions, five occur both in South Africa and other parts of the world, namely (1) tropical and subtropical moist broadleaf forests, (2) tropical and subtropical grasslands, savannas and shrublands, (3) montane grasslands and shrublands, (4) Mediterranean forests, woodlands and scrub and (5) deserts and xeric shrublands.

For the projection of South African biomes throughout the world, we used the biome map recently compiled following a rigorous regional vegetation mapping exercise (Mucina & Rutherford, 2005). This map is the best-available data set of its kind at a scale appropriate for this study. Seven biomes have been used for South Africa, namely, (1) desert, (2) succulent karoo, (3) Nama-karoo, (4) fynbos, (5) Albany thicket, (6) grassland and (7) savanna. Because savanna and grassland extend beyond South Africa, we extended our analysis to two neighbouring countries (Namibia and Botswana) to better capture the full climatic

determinants of these biomes, thus avoiding truncated response curves in the models (Austin & Gaywood, 1994; Thuiller *et al.*, 2004). The polygons were then rasterized at $10' \times 10'$ grid resolution to match the climatic data sets.

Distribution data for the South African plant species were extracted from the PRECIS (Germishuizen & Meyer, 2003) and Ackdat (Rutherford *et al.*, 2003) databases, which contain georeferenced data for more than 27 000 plant taxa. The Ackdat database is constituted of real presence/absence locations, while PRECIS contains only presences. However, taking into account the spatial resolution used in this study ($25 \times 25 \, km^2$), as well as the relatively good surveys, we assume that absences in PRECIS (i.e. where a particular species has not been recorded) are reliable. We selected 96 plant taxa endemic to South Africa and known to be invasive in other parts of the world (see Appendix A) to conduct this analysis. We selected species known to be invasive as they provide a way to quantify and test the degree of accuracy of the proposed approach. Attention was also paid to selecting a good cross-section of taxa in terms of life form and natural distribution across South African biomes. Species data sets were extracted at quarter-degree scale resolution (QDS, $\sim 25 \times 25 \, km^2$).

For bioclimatic data, the CRU CL 2.0 global data set at $10' \times 10'$ served as the base data set (New *et al.*, 2000), to ensure that data set consistency did not affect the analysis. Three variables known to affect plant physiology and growth (Bartlein *et al.*, 1986; Woodward, 1987) were derived for the study: growing degree days (base 5); minimum temperature of the coldest month; and an index of humidity (AET/PET: mean ratio of annual actual over annual potential evapotranspiration). Potential evapotranspiration estimates were calculated using the FAO 56 Penman Monteith combination equation (Allen *et al.*, 1998), while actual evapotranspiration estimates were derived using the LPJ dynamic global vegetation model (Hickler *et al.*, 2004). Although these annual variables are key determinants for plant physiology, they provide no quantification of consistent interannual patterns such as those occuring in (1) mediterranean-type climates (Southern Europe, California, South Africa, Chile and Australia) with wet cool winters and hot dry summers, (2) seasonal subtropical rainforests with hot wet summers and cold dry winters or (3) temperate areas with hot wet summer and cold wet winters. To deal with this problem, we computed a fourth variable, namely plant productivity index (PPI): the number of months per year receiving more rainfall than twice the mean annual temperature for that site, which provides a surrogate for the rainfall seasonality and the length of the growing season (le Houérou,

1984). This categorical variable (from 0 to 12 months) gives a relevant measure of seasonality for our analysis.

In the case of the species modelling approach, and because of the coarser resolution of the species data sets, we upscaled the $10' \times 10'$ grids to QDS resolution.

Biome distribution models

The observed biome distributions in South Africa were exclusive in the sense that only one biome can occur in one given site (one categorical variable). To model the distribution of biomes, we constructed a disjunctive table from the categorical variable and modelled each biome independently.

Generalized additive models (GAM, Hastie & Tibshirani, 1990) incorporated into the Splus-based BIOMOD application (Thuiller, 2003), relating the biome distributions to the four bioclimatic variables, were calibrated using a random sample of the data (70%) and a stepwise selection methodology, with the most parsimonious model being selected using the Akaike information criterion (AIC) (Akaike, 1974). The use of GAM in biogeographical studies is not new, and they have been widely tested and compared with other distribution models (Elith, 2000; Thuiller, 2003; Segurado & Araújo, 2004). These studies and others have shown that because of their nonparametric nature, they can mimic different types of response curves and provide a better alternative than most other widely used models like generalized linear models or classification tree analysis (Araújo *et al.*, 2005).

To validate our prediction in South Africa, the predictive power of each model was evaluated on the remaining 30% of the data using the values obtained for the area under the curve (AUC) of a receiver–operating characteristic (ROC) plot of sensitivity against $(1-$sensitivity$)$ (Swets, 1988). Sensitivity is defined as the proportion of true positives correctly predicted, whereas specificity is the proportion of true negatives correctly predicted. We used the following conservative rough guide for AUC<0.8: null model; $0.8<$ AUC <0.9: fair model; $0.9<$AUC<0.95: good model; $0.95<$AUC<1: very good model.

The different models calibrated in South Africa were then used to project the potential analogous areas throughout the world. As the biomes were modelled individually and provided the probability of occurrence for each biome over the whole world, we defined the potential biome as the one with the highest probability of occurrence in a given place. To achieve this, each pixel was evaluated and assigned to the biome with the highest probability of occurrence. This approach was based on the assumption that, without human influence, the dominant vegetation type in a given area should have the highest probability to occur. Unfortunately, the worldwide biome projections cannot be validated, as they do not actually exist outside of their native range. However, they do provide an insight into where similar biomes can host invasive species from the particular South African biomes.

Species' distribution models

Our approach to modelling species' distributions was similar to that for the biomes, and was based on ecological niches (Guisan & Zimmermann, 2000; Peterson, 2003; Guisan & Thuiller, 2005). Because we used only bioclimatic variables, we modelled the bioclimatic niche of the species. Our approach comprised four steps: (1) model the bioclimatic requirements of the species based on known occurrences in the native distribution area of the species in South Africa; (2) test the accuracy of the native-range predictions; (3) project the model over the world to identify areas potentially susceptible to invasion; and (4) validate predictions in other regions.

We used the same modelling approach as for the biomes (GAM procedure under the Splus-based BIOMOD application, Thuiller, 2003, 2004). Models were also calibrated using 70% of the initial data sets and evaluated on the remaining 30% using the ROC curve procedure. We then projected these validated native-range bioclimatic niche models for species worldwide to evaluate the areas most susceptible to invasion. For the worldwide species projections, as absence data were not available, models for some species and some specific areas with observed presence available were validated by χ^2-tests (Peterson *et al.*, 2003; Peterson & Shaw, 2003) that incorporate dimensions of correct prediction of both presences (based on independent test data) and absences (based on expected frequencies) (Roura-Pascual *et al.*, 2004). Here, random expectations were calculated as the product of the proportional area predicted present and the number of test presence points. Observed frequencies of correct and incorrect predictions of presence were then compared using a χ^2-test (1 df).

Invasion risk assessment

To provide a broad estimate of risk, we compiled a surface of cumulative risks probabilities, comprising the sum of probability surfaces for the 96 taxa. Species-specific probabilities were rescaled to a range of 0–1 for standardization. This cumulated probability surface was used to produce a global risk map for invasive species of South African origin.

To assess the validity of such a pro-active approach by using real data, we related the cumulated probability map to the number of South African species reported as invasive throughout the world. The data were extracted from Weber (2003). This global overview lists species invasive in natural areas (following the definition of the IUCN) and naturalized outside natural areas; summing these two categories gives a comprehensive estimate of the total number of naturalized species (sensu Richardson *et al.*, 2000b) in nine regions of the world. Species of South African origin are best represented in Australia (47 invasive in natural areas, 50 naturalized in total), North America (15, 30), Europe (6, 20) and South America (4, 17), less in tropical and North Africa (0, 16), tropical Asia (1, 10) and temperate Asia (0, 4).

To incorporate the effect of international dispersal opportunities of South African species, we quantified variables that can be assumed to relate to the propagule pressure (i.e. trade and tourism). We used information on the number of tourists from other countries visiting South Africa and the volume of trade concerning exportation of living plants from South Africa towards other countries. Tourism data were extracted as a 3-year total (2000–2002) from the 'Statistics South Africa Annual Report-03-51-02 – Tourism' (http://www.statssa.gov.za). For living plants, the 'South African Trade HS 4 DIGIT Codes', in particular, 'Chapter 6 – Live trees and other plants, bulbs, roots and the like, cut flowers and ornamental foliage' (http://www.dti.gov.za) were used to compile the figures for trade in live plant specimens. Here, a 3-year total was also used, but for the 2001–2003 period.

Finally, we tested whether the combination of propagule pressure and climatic suitability allows prediction of the number of South African species invasive in other parts of the world. Although this test is limited by the recent nature of trade and tourism volume estimates, while the current global distribution of alien species is a result of processes over the past two to three centuries (but largely the last century), we believe that it is a reasonable surrogate of past historical events (reliable historical data on trade and tourism are not readily available). Those parts of the world with the closest recent trade links with South Africa (Europe, Australia, North America) have also formed the axes of the most important trade routes since Colonial times, with a major impact on current biological invasions (Crosby, 1986; Kruger *et al.*, 1989). Moreover, the recent data are likely to be a good indicator of current trends in propagule pressure and are thus very useful for defining how current trade could influence invasions in the future.

Results

Ecoregion mapping

Five ecoregions occur both in South Africa and other parts of the world (Fig. 1a). According to this approach, almost all of Africa appears suitable for South African plant species, mainly savanna and xeric shrubland species, as well as tropical and subtropical grassland species. South America is also predicted to be potentially invasible, mainly in the tropical northern part. The extreme western part of this continent is predicted to be suitable for South African mediterranean forest or scrub species, as well as species from xeric shrubland. North America is predicted to be suitable for South African species only in its western part, represented by Mediterranean forest in the Californian Floristic Region and xeric shrublands further inland. Europe is predicted to be suitable only for woodland and scrub in the Mediterranean Basin. Australia shares Mediterranean woodland and scrub, xeric shrubland and savanna with South Africa, these three ecoregions covering most of Australian territory; only its extreme south-eastern part is predicted to be unsuitable for South African species. Asia is predicted to be suitable for savanna and grassland species, and the Middle East for xeric shrubland species.

Biome distribution models

The predictive accuracy of biome distribution models, based on their native distribution, is summarized in Table 1. The best results were obtained for desert, grassland and savanna with *ca.* 95% of both presences and absences correctly predicted. Albany thicket was predicted with the lowest accuracy of *ca.* 90% of correct predictions, reflecting difficulties in conceptualizing this biome in climatic terms (Cowling *et al.*, 2005; Mucina & Rutherford, 2005). It should be noted that a high predictive accuracy could be expected as the definition of biomes is based on both vegetation structure and climatic similarity.

Despite some similarities with the ecoregion mapping (Fig. 1a), global projection of South African biomes highlighted some interesting differences (Fig. 1b). The south-western part of Australia, predicted as unsuitable by the ecoregion approach, appears suitable for South African species of grassland, fynbos and succulent karoo. Temperate Europe and the south-eastern part of the USA now appear suitable for South African grassland species, although predicted unsuitable by the ecoregion mapping.

South America exhibits the most disagreement between the two approaches. Its northern part, con-
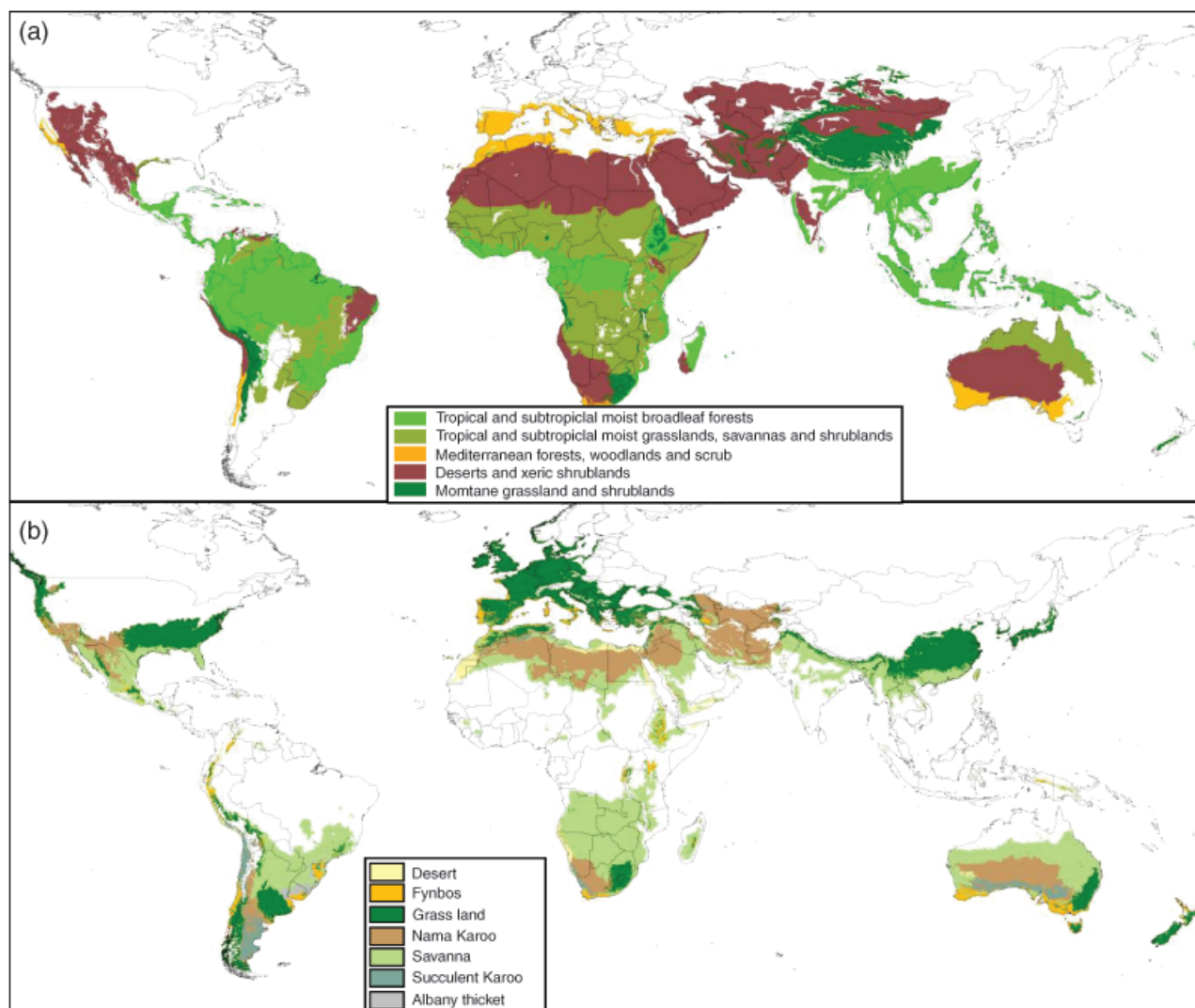
Fig. 1 (a) Mapping of the ecoregions occurring in both South Africa and other parts of the world. (b) Worldwide projection of South African biomes using the generalized additive model calibrated in South Africa. The projected biome is the one with the highest probability of occurrence for a given pixel.

sidered as suitable for South African species according to the ecoregion mapping, appears completely unsuitable with the biome distribution model approach. In the south, the situation is contrasting, this part now being predicted suitable for various South African biomes. In South America, the only agreement concerns Mediterranean-climate parts of Chile, which are predicted to be suitable for fynbos species by both approaches.

China and India exhibit similar patterns using both approaches, with parts suitable for grassland and savanna species. Both approaches also identified similar suitable biomes in Northern Africa, like xeric shrublands (succulent karoo, Nama-karoo and dwarf savanna).

Species' distribution models

Native distribution of South African species. The predicted distributions of the 96 selected plant taxa (Appendix A) show a very good general agreement with the observed distributions (Table 2), with the median percentage of presences and absences correctly predicted as 90.5% and 90.8%, respectively.

The modelled species with the lowest predictive accuracy (AUC = 0.68) is *Malephora lutea* (Aizoaceae). The models had a very high predictive accuracy for the calibration data set (AUC = 0.98), demonstrating an overparameterization and the difficulty for the model in defining a simple combination of environmental variables to delimitate its distribution. The modelled

Table 1 Predictive accuracy of the biome distribution models in South Africa for the seven modelled biomes

	AUC			% of presences correctly predicted	% of absences correctly predicted
	Calibration	Evaluation	Total		
Desert	0.99	0.99	0.99	96.58	96.50
Succulent karoo	0.99	0.94	0.97	94.57	94.56
Nama-karoo	0.97	0.95	0.96	90.38	90.38
Fynbos	0.98	0.98	0.98	92.13	91.95
Albany thicket	0.96	0.97	0.97	89.90	89.51
Grassland	0.99	0.99	0.99	96.27	96.30
Savanna	0.99	0.99	0.99	94.78	94.78

AUC represents the area under the ROC (receiver–operating characteristic) curve, estimated for the calibration, evaluation and the original data set.

Table 2 Summary of the predictive accuracy of the species' distribution models in South Africa carried out on 96 selected species (endemic to South Africa and invasive elsewhere; Appendix A)

	AUC			% of presences correctly predicted	% of absences correctly predicted
	Calibration	Evaluation	Total		
Minimum	0.75	0.68	0.76	67.24	68.40
First quartile	0.94	0.88	0.92	85.80	86.61
Median	0.97	0.94	0.96	90.48	91.00
Third quartile	0.99	0.97	0.97	92.98	93.29
Maximum	1.00	1.00	1.00	100.00	98.32

AUC represent the area under the ROC (receiver–operating characteristic) curve, estimated for the calibration, evaluation and the original data set.

species with the highest predictive accuracy (AUC = 1) is *Senecio glastifolius* (Asteraceae), reported as invasive in New Zealand and Australia (Weber, 2003).

Adventive distribution of selected South African species. The high predictive accuracy of our models provides justification for projecting the potential climatic space suitable for each of the 96 modelled taxa globally. As data on the current secondary distribution ranges are not available for all these species, we assessed the projection accuracy using three examples, for which information on adventive distribution is sufficiently detailed. These three species were selected as representing different life forms, regions where invasive and history of invasion, hence highlighting different invasion dynamics.

Carpobrotus edulis (Aizoaceae) is a succulent endemic to the Cape Floristic Region and has a long history of invasion in Europe, California, Australia, South America and New Zealand (Weber, 2003). Its potential geographical range was evaluated in Europe (data extracted from the Atlas Florae Europaeae, Jalas & Suominen (1972–1996)) and Australia (observed data

extracted from the Australian Virtual Library Project 2004) (Fig. 2a). The projection of potentially suitable habitats in the secondary distribution range showed considerable agreement with recorded presences (χ^2-test, $P < 0.001$). The projections suggest that this species has already invaded most suitable habitats in Europe, although some areas with the highest probability of occurrence (Portugal, Corsica) could be invaded more extensively in the future. In Australia, the projection fits very well with the recorded presence; some areas with high suitability could be susceptible to invasion if not already invaded. For instance, the south-eastern coast exhibits a very high probability of occurrence but the species has currently only invaded areas along the coast and few inland sites. Other areas identified as having a high probability of potential distribution of *C. edulis* include the western coast of Chile and the Atlantic coast of the USA (Fig. 2a), where it has already been recorded (Vilà & D'Antonio, 1998) but digitized distributions are not available for South America. Invasion of *C. edulis* is also predicted in central east Africa, harbouring ecoregions and biomes suitable for invasion by South African plants of savanna, grassland and fynbos (Fig. 1).
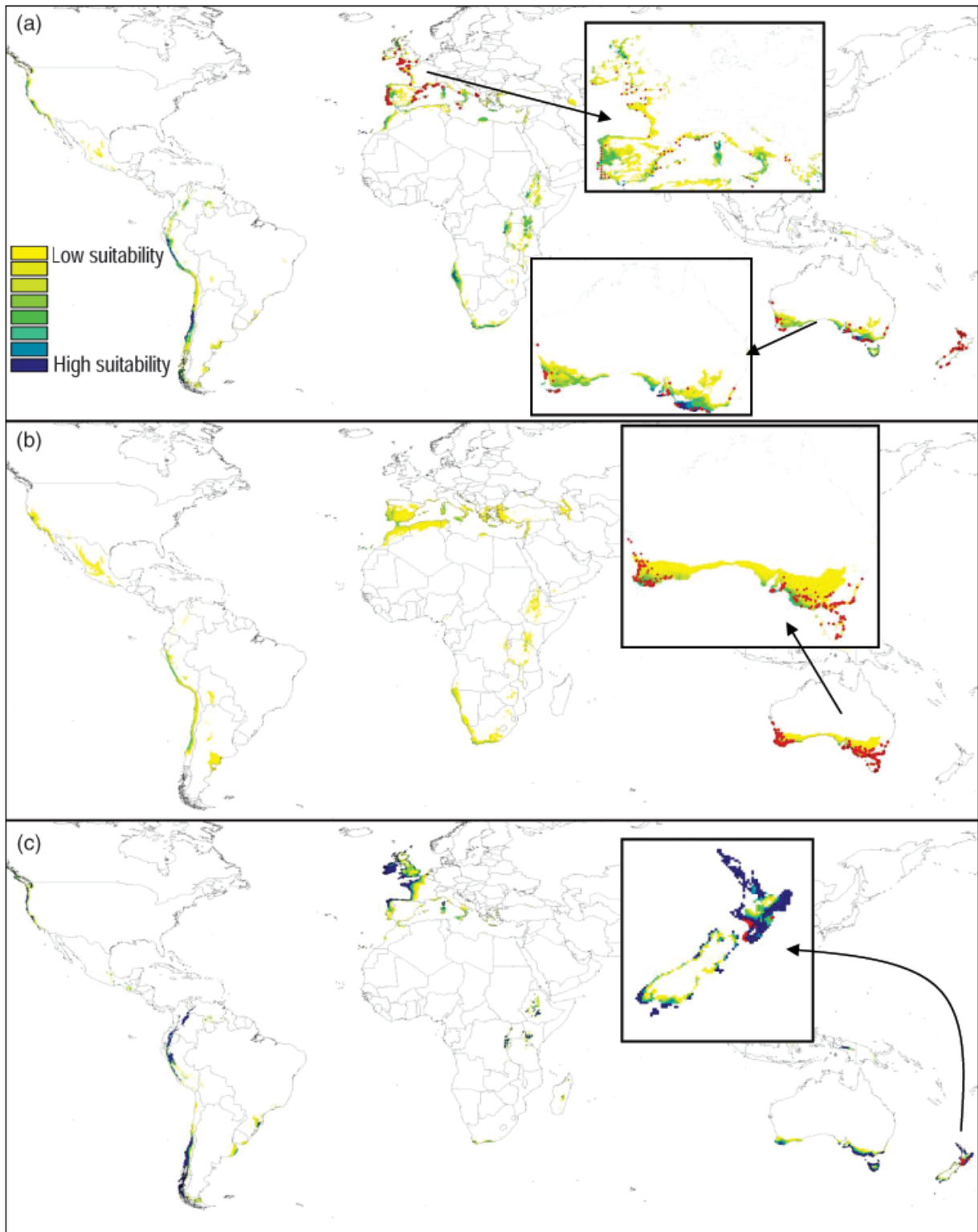
Fig. 2 Worldwide projection of potential habitat of (a) *Carpobrotus edulis*, (b) *Vellereophyton dealbatum* and (c) *Senecio glastifolius* (ranking from 0 to 1), and the observed records of the species in some invaded countries (red dots).

Vellereophyton dealbatum (Asteraceae) is an annual or short-lived perennial widespread in South Africa. Its distribution was accurately mapped in Australia (Australia Virtual Herbarium Project 2004), allowing precise testing of our projection (Fig. 2b). The suitability surface predicted in Australia and the observed presence for this species show remarkable agreement (χ^2-test, $P < 0.001$); most of the highly suitable areas, and some of the medium-suitability areas have already been invaded. The worldwide projection indicates that climatic suitability space for this species is limited, with the highest potential in Portugal, Sicily and Chile (Fig. 2b).

Our last example is *Senecio glastifolius* (Asteraceae), a tall perennial herb endemic to the Cape Floristic Region. It was introduced to New Zealand as recently as 1963 (observed data extracted from Williams *et al.*, 1999). For several decades, it remained largely confined to a few ruderal sites in the southern North Island, but now it occupies a wide range of mostly coastal sites, where it recently began to spread dramatically (Williams *et al.*, 1999). The observed distribution of the species was well predicted (χ^2-test, $P < 0.05$), despite large areas with high probability of occurrence without known observed presence (Fig. 2c). These areas with high probability, but no observed presence, could be sites not yet invaded, could be false positives or could be unsampled invaded areas. These bioclimatically suitable areas, likely to be invaded in the future, include a large part of the North Island, and some coastal areas of the South Island. Nevertheless, it is likely that the potential distribution could be overestimated knowing the altitudinal heterogeneity of New Zealand, which is not included in our analysis because of the coarse resolution.

The worldwide potential distribution of this species highlights other areas highly susceptible to invasion: south-east and south-west of Australia and Tasmania, Atlantic coast of Spain and France, Ireland and Great Britain and the western coast of Chile (Fig. 2c). Despite the lack of distributional data, this species is currently of major concern in Australia – it is known to be naturalized in New South Wales and Western Australia (Williams *et al.*, 1999), and is classified as a 'sleeper weed' (i.e. thought to have much potential to expand its range). It is on the 'National Alert List' in Australia and is listed among the 'The ten most serious invasive garden plants currently available for sale by nurseries in New South Wales' (Groves *et al.*, 2005).

Invasion risk assessment

A cumulative probability surface, comprising the sum of probability surfaces for the 96 taxa and rescaled to a range of 0–1, highlights parts of the world highly susceptible to invasion by South African plant species (Fig. 3). Areas most susceptible to invasion are mainly in the Southern Hemisphere, extensively in southern Australia and the western coasts of South America. In the Northern Hemisphere, the Mediterranean Basin is at highest risk, along with the southern part of Great Britain. Globally, these highly invasible areas encompass six biodiversity hotspots, namely Mediterranean Basin, California Floristic Province, Chocó-Darién Western Equator, Central Chile, South-west Australia and New Zealand.
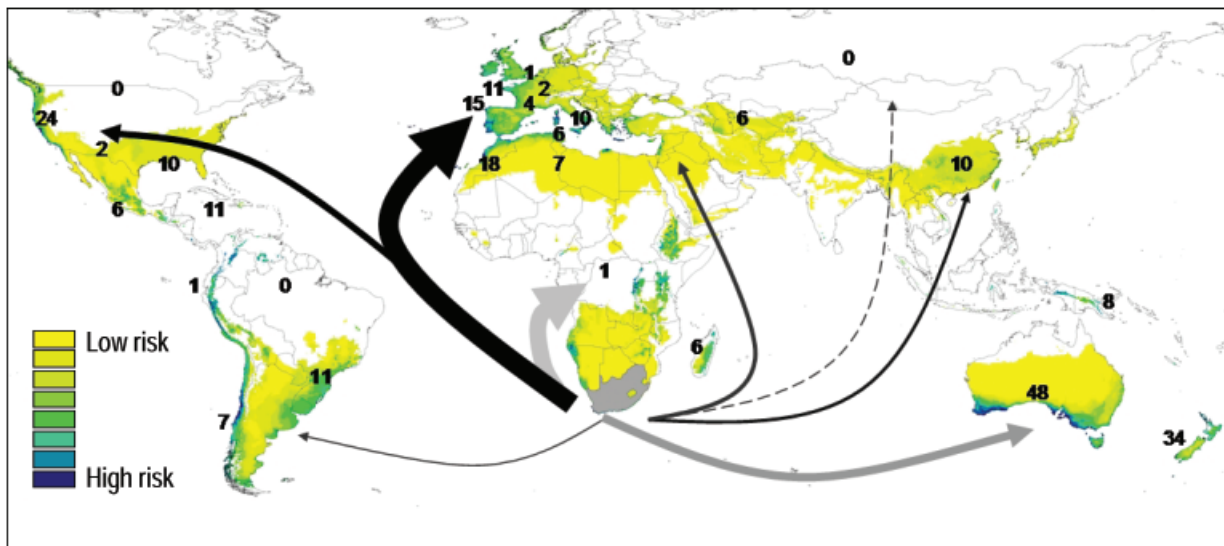

Fig. 3 Cumulated probabilities from the risk assessment. Low-to-high-risk areas are mapped from yellow to dark blue. Numbers indicate the number of South African plant species recorded as invasive in natural areas in the given region (from Weber, 2003). Arrows indicating propagule pressure increase in thickness with increasing tourism and range from grey to black with increasing trade in live plant products.

Climate match and propagule pressure as predictors of invasions by South African plants

Visual inspection of areas at high risk of invasion by South African plants and of the global recent distribution of invasive species of South African origin indicates a good match. The highest concentration of invasive South African plants is found in Australia, European Mediterranean and the Pacific coast of USA (Fig. 3). The western coast of Chile is the only region with a high probability of invasion that has received a limited number of species from South Africa. In general, there are no realized invasions into regions that are climatically unsuitable (northern South America, northernmost part of North America, central part of Africa and most of Asia except for the south-eastern part).

To test the relationship between the potential occurrence of South African alien species and climatic habitat suitability (Fig. 3), we used data from those subregions from which at least one South African species was reported as invasive (Weber, 2003), assuming that where none were present, it was because of low propagule pressure (Lonsdale, 1999). We found a significant positive relationship between the number of South African species invading natural habitats in a given region and its habitat suitability ($F = 7.14$, df $= 8$, $P = 0.0282$, $R^2 = 0.47$). However, this only holds for invasive species in natural areas; the total number of naturalized (including outside natural areas) South African species was not significantly related to habitat suitability for the subregion. The relationship between the percentage of species invading natural areas, of the total of naturalized aliens, and climate-based habitat suitability, using the same data was also significant ($F = 7.40$, df $= 8$, $P = 0.0262$, $R^2 = 0.48$).

To investigate the combined effect of climatic suitability and other factors, we added the extent of trade and tourism between South Africa and respective regions, as a proxy for propagule pressure (Fig. 3). Neither of these additional variables appeared to predict the number of naturalized South African species. However, if the relative proportion of trade on the combined measures (trade + tourism) is used, the percentage of species invading natural areas for all South African naturalized aliens in a region increased with both habitat climatic suitability and the percentage of trade. The relationship was highly significant ($P = 0.0044$) and explained 78.7% of variation in the data. Therefore, the higher the proportion of trade, the greater the likelihood of the incorporation of commercially distributed and suitably preadapted alien species of South African origin into the natural vegetation of a recipient region.

Discussion

Niche-based models as a tool for predicting distribution of invasive species

Our approach is based on the assumption that climate is the major driving factor of species' distribution (Woodward, 1987), and that analysis of the climatic preferences of a species can therefore be used to predict areas where the species could occur at regional, continental and global scales. Although climate sets the broad limits of plant species' ranges, other factors such as geology, soils, disturbance regime, competition and other biotic interactions determine the presence or absence of a species in a particular area and at finer (i.e. regional or local) scales (Willis & Whittaker, 2002). In the same vein, climate principally affects the global distribution of invasive species as they can only succeed in regions where they are not limited by climatic constraints to survival, establishment and reproduction (Panetta & Mitchell, 1991; Scott & Panetta, 1993). However, other factors need to be included in models at a finer geographical scale to predict the distribution of invasive aliens, among which propagule pressure and disturbance are of major importance (Rouget & Richardson, 2003; Huston, 2004). Unfortunately, these other factors are rarely taken into account because accurate maps at an appropriate scale are very seldom available.

An additional limitation, at least for the biome and species' distribution modelling approach, is that the observed distribution in the native range need not represent the complete realized niche of the modelled entity, thus preventing the full capture of the climatic determinants of the distribution. Historical events, dispersal limitation or biotic factors can prevent species from occupying their full climatic ranges (Svenning & Skov, 2004). Nevertheless, at the scale and resolution of our data set, the selected endemic species are close to equilibrium with climate, and the projections worldwide are not spurious as evidenced by testing based on the observed occurrence of those species.

Finally, potential global distributions of species are projected on the assumption that current climatic niches reflect species' environmental preferences, which will be retained in the invaded new areas. This principle has strong support from studies demonstrating the evolutionary conservatism of ecological niches and the phylogenetic inertia of species across time scales (Peterson *et al.*, 1999) as well as from comparative biogeographical studies (Huntley *et al.*, 1989; Beerling *et al.*, 1995, but see Maron *et al.*, 2004 for a counter-example).

Comparing ecoregions, biomes and species' distribution approaches

The ecoregion mapping is the simplest screening approach, but the very coarse definition of the ecoregion (Olson *et al.*, 2001) leads to unreliable results in terms of predicting areas to be potentially invaded. For example, this approach identified some areas in western and central Europe and south-western Australia as unsuitable for South African species; yet, many are present there (Weber, 2003), among them two species investigated in detail in our study (*Carpobrotus edulis* and *Vellereophyton dealbatum*). The ecoregion definition is clearly too broad to be effective for screening purposes at a scale that is useful for management.

The biome distribution modelling approach is much better, although still very simple. Compared with the ecoregion mapping, it correctly identified areas (Europe north of the Mediterranean, the western USA, and parts of Africa, Australia and the Middle East) where invasive plants from South Africa are known to occur. Of course, global climatic data sets and sufficiently detailed biome maps for the donor areas are necessary prerequisites, but this is not a major constraint for most regions, given the increasing availability of global data sets and mapping projects. Most of the projected biomes fit very well with their actual distribution throughout the world. The biome approach therefore appears to be reliable enough to provide the first-step screening of alien plants.

There are, however, some drawbacks similar to those experienced in the ecoregion mapping. The reliability of the biome approach depends on how particular biomes are defined in the donor country; given the complexity of measures used in these definitions, local differences in classification can generate problems (Smith, 1974; Rutherford & Westfall, 1994). Biome distributions are also not exempted from historical and stochastic events. This can be illustrated with reference to our analysis of the grassland biome in South Africa. The GAM models project grassland over most of Europe (Fig. 1b), most of China and the north-western coast and south-east of the USA. These areas are in fact mainly covered by forest or temperate woodland. The intensity and frequency of fire in South African grassland shed some light on such anomalous projections. Several analyses hypothesized that without fire, the grassland biome should be forest, but that the intensity and especially the frequency (~ 10 years) of fires preclude tree establishment and encroachment (Bond *et al.*, 2003). Given this, the projection of grassland in some areas currently dominated by trees but lacking frequent fire is explicable.

If species' distribution data in the donor country are available, climatic niche modelling offers a powerful tool for efficient and unbiased first-step screening of multiple species. The major advantage is that this approach is taxon specific, and hence finer and more robust than broad screening based on ecoregion mapping. If a taxon is already invading, the identification of new potential sites of invasion is required and the approach can help to guard against further introductions and the initiation of new invasion foci. Given that eradication of an established invasive species is extremely difficult, and usually impossible (Rejmánek & Pitcairn, 2002), areas identified as potential new sites should be monitored and quarantine measures should be adopted. A species' potential distribution is generally more extensive than its actual distribution (Peterson *et al.*, 2002). This may result from invasion potential not yet realized, insufficient knowledge or additional distribution-restricting factors such as existence of allopatric sister species, interspecific competition, previous extinctions and limited dispersal abilities (Peterson, 2003). Some of these factors, namely insufficient knowledge and presence of potential competitors, are also applicable as limits to the realized distribution in the native range.

The use of the three species adventive distribution that we analysed in detail illustrates that the worldwide projection of the native range based on the ecological niche model has considerable predictive power. The areas of underprediction (i.e. where predictions are negative but the species is known to be present) are minor and correspond to urban localities where the occurrence may be because of the subsidy of human influence. Although predictions in some areas underestimated or overestimated the species' invasion potential, their ability to identify key distribution areas was clearly much better than that of random models, or simple biome mapping presented above.

Climate-match and propagule pressure as determinants of invasions

For a global risk assessment of invasions by South African alien species, we combined the information from the species' distribution models to deduce the areas that may be most susceptible to invasion by South African species. The risk-assessment map shows significant agreement with the observed number of invasive species from South Africa. That a significant effect of climate-based habitat suitability was only found for invasive species in natural areas and not for all naturalized South African indicates that outside natural areas, factors other than climate, play a role. It may be hypothesized that human activities resulting in intense propagule pressure and high levels of disturbance are of overriding importance, biasing the

relationship between invasions and climate. That the climatic match is the main filter determining which species of the total pool of naturalized aliens become successful invaders of natural habitats is demonstrated by a significant relationship between the percentage of species invading natural areas, of the total of naturalized aliens and habitat suitability.

In addition, by incorporating information on propagule pressure, we demonstrate that invasions can be predicted globally with a reasonably high precision. This is probably only possible if the source–area approach based on the known species pool is used, as this eliminates biases resulting from different likelihoods of species reaching given target areas (Pyšek et al., 2004). Although our index of propagule pressure was based only on the recent pattern of global exchange, in combination with our climate-derived risk assessment, it showed a very good predictive accuracy and explained a large proportion of variation in the current numbers of South African invasive species. In addition, as the assessment of propagule pressure is based on recent data, it provides an estimate of what is likely to happen in the near future. Our risk assessment demonstrates that most of the southwestern part of Europe is potentially suitable for invasion by South African species. This, together with a high intensity of tourism between Europe and South Africa, and massive imports of plant material to the former continent make Europe potentially vulnerable to invasions by more South African plants in the future. A similar pattern can be assumed for Australia and the United States. On the contrary, China and South America are also climatically suitable for South African species, but there is quite low exchange of trade and tourism with these regions. This explains the currently low representation of South African invasive species in these regions (e.g. Castro et al., 2005; Liu et al., 2005), and also makes these regions potentially less prone to invasions by South African plants in the near future.

Towards a more precise prediction of plant invasions

There are several assumptions of a successful invasion, along the lines of phases of the invasion process (Richardson et al., 2000b): (1) dispersal opportunities that allow species to reach new areas; (2) ecological suitability of the new habitat, and overcoming biotic and abiotic barriers constraining; (3) naturalization in and; (4) spread across the new region (Hobbs & Humphries, 1995; Rejmánek et al., 2005). Prediction of the actual course of an invasion requires a detailed understanding of all four components. Each invasion may be potentially rapid and unstoppable, but in

reality it is constrained by the ecological niche of the invading species, defined by the suitability area. While the spread can be so dynamic as to make the modelling of contagion irrelevant, the equilibrium spatial pattern can be quite predictable if the ecological niche of the invading species is well understood (Peterson & Vieglais, 2001).

The approach presented here provides a sound and tested possibility to predict one of them: climatic suitability (Zalba et al., 2000; Welk et al., 2002; Peterson, 2003; Roura-Pascual et al., 2004). The close match that we found between the climatic component of the ecological habitat suitability and the current pattern of occurrence of South African alien species in other parts of the world is encouraging and highlights the pivotal role of climate for predictions at the global scale. In addition, present invasions of South African species around the world can be reasonably well explained by surrogates for propagule pressure based on trade and tourism. These data are available globally, and their implementation provides the possibility of taking the dispersal component into account in predictive models. It should also be noted that a much better explanatory power of these variables could have been achieved if data on the global distribution of invasive species were available at a scale comparable with the climate data; unfortunately, such fine-scale data are still scarce, despite the promising emergence of regional databases such as BioFlor (Kühn et al., 2004).

Invasion potential can be identified and assessed before an invasion takes place, as has been implemented in invasive species monitoring schemes at the national and state level in Australia (Thorp & Lynch, 2000). A first strength of this approach is to detect critical source areas for new invasives. This could be used for specific quarantine procedures in the case of products arriving from these regions (e.g. Thorp & Lynch, 2000). Finally, the main strength of our approach lies in that it can identify key geographical areas that are highly susceptible to invasions, based on geographical and economic data. This capacity could substantially improve management efforts for particular species once they have been detected outside their natural ranges. Because biological invasions are part of global change and as changes in species' distributions alter global biodiversity (Vitousek et al., 1997; Chapin et al., 2000; Sala et al., 2000), procedures for identifying potential new areas for invaders must be incorporated into integrated strategies for reducing invasions. To incorporate the phases of naturalization and spread, screening of life-history attributes would further improve the accuracy of prediction and become the next significant step on the way to preventing future invasions from alien species.

Acknowledgements

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Appendix A

Taxa selected for the bioclimatic niche-based modelling approach. Family, life form and biomes in which the taxon occurs in South Africa are shown. For taxa that occur in several biomes (marked Multi), the subsequent biomes are listed in the next column (Details for multi). The last column lists countries and regions where the taxa are known to be naturalized or invasive (D. M. Richardson, personal observation, L. Henderson and R. P. Randall, personal communication). Not all South African plant taxa known to be invasive elsewhere were used – only those for which at least 20 accurate distribution records from South Africa were available were included (Table A1).

Table A1

Taxon	Family	Life form	Main biomes	Details for multi	Invaded countries/regions
Agapanthus praecox	Liliaceae	PH	Multi	AT, F, S	Australia
Agapanthus praecox spp. orientalis	Liliaceae	PH	Multi	AT, F, G, S	Australia
Agathosma crenulata	Rutaceae	shrub	F		Australia
Aloe striata	Aloaceae	Succ	Multi	AT, G, Nk	USA
Amaryllis belladonna	Amaryllidaceae	PH	F		Australia, Chile, Europe, NZ, USA,
Aponogeton distachyos	Aponogetonaceae	PH	F		Europe, NZ, USA
Arctotheca populifolia	Asteraceae	PH	Multi	AT, F, Sk	Australia
Arctotis stoechadifolia	Asteraceae	Shrub	Multi	F, Nk, Sk	Australia, USA, NZ
Asparagus scandens	Asparagaceae	Climbing perennial	F		Australia, NZ
Babiana disticha	Iridaceae	PH	F		Australia
Babiana striata	Iridaceae	PH	F		Australia
Babiana tubulosa	Iridaceae	PH	F		Australia
Baeometra uniflora	Colchicaceae	PH	F		Australia
Berkheya rigida	Asteraceae	PH	Multi	F, G, Nk	Australia
Carpobrotus acinaciformis	Aizoaceae	Succ	F		Mediterranean Basin, USA
Carpobrotus edulis	Aizoaceae	Succ	F	AT, Sk	Australia, Europe, NZ, USA
Chasmanthe floribunda	Iridaceae	PH	F		Australia, USA
Chrysanthemoides monilifera	Asteraceae	Succ	Multi	F, G, S, Sk	Australia, Europe, NZ
Chrysanthemoides monilifera spp. moniflora	Asteraceae	Succ	F	AT, G	Australia, Europe, NZ
Conicosia pugioniformis	Aizoaceae	Shrub	Multi	F, Sk	Australia, USA
Cotula turbinata	Asteraceae	PH	F		Australia
Cotyledon orbiculata	Crassulaceae	Succ	Multi		Australia, USA
Crassula multicava	Crassulaceae	Succ	AT	S	Australia
Cyperus textilis	Cyperaceae	AG	Multi	AT, F, G, S	Europe
Dietes grandiflora	Iridaceae	PH	Multi	AT, F, G, S	Australia
Dipogon lignosus	Fabaceae	Woody climber	Multi	AT, F, G, S	Australia, NZ

(Continued)

Table A1. (Contd.)

Taxon	Family	Life form	Main biomes	Details for multi	Invaded countries/regions
Dischisma capitatum	Scrophulariaceae	AH	F		Australia
Ehrharta erecta	Poaceae	PG	Multi		Australia, Hawaii, USA
Ehrharta longiflora	Poaceae	AG	Multi	F, Sk	Australia
Euryops abrotanifolius	Iridaceae	PH	F		Australia
Ferraria crispa	Iridaceae	PH	F		Australia
Freesia alba	Iridaceae	PH	F		Australia
Freesia refracta	Iridaceae	PH	F		USA
Galenia pubescens	Aizoaceae	PH	Multi		Australia, Chile, USA
Gazania linearis	Asteraceae	PH	Multi	G, Nk, S	Australia, NZ, USA
Gazania rigens	Asteraceae	PH	Multi	Nk, Sk	Australia, NZ, USA
Gladiolus alatus	Iridaceae	PH	F		Australia
Gladiolus angustus	Iridaceae	PH	F		Australia
Gladiolus carneus	Iridaceae	PH	F		Australia
Gladiolus caryophyllaceus	Iridaceae	PH	F		Australia
Gladiolus tristis	Iridaceae	PH	F		Australia, USA
Gladiolus undulatus	Iridaceae	PH	F		Australia, NZ
Gorteria personata	Asteraceae	PH	F		Australia, NZ
Grammatotheca bergiana	Campanulaceae	AH	F		Australia
Hebenstretia dentata	Scrophulariaceae	AH	Multi		Australia, Europe
Helichrysum petiolare	Asteraceae	Shrub	Multi	AT, F, G	Europe, NZ, USA
Heliophila pusilla	Brassicaceae	AH	F		Australia
Hesperantha falcata	Iridaceae	PH	F		Australia
Holcus setiger	Poaceae	AG	F		Australia
Ixia maculata	Iridaceae	PH	F		Australia, USA
Ixia paniculata	Iridaceae	PH	F		Australia
Kniphofia uvaria	Liliaceae	PH	Multi	AT, F, G	Australia, Europe, USA
Lachenalia aloides	Hyacinthaceae	PH	F		Australia
Lachenalia bulbifera	Hyacinthaceae	PH	F		Australia
Lachenalia mutabilis	Hyacinthaceae	PH	Multi	F, Sk	Australia
Lampranthus spectabilis	Aizoaceae	Succ	F		NZ
Leonotis leonurus	Lamiaceae	Shrub	Multi	F, G	Australia
Malephora crocea	Aizoaceae	Shrub	Multi	F, Nk, Sk	USA
Malephora lutea	Aizoaceae	Succ	F	AT, Sk	Australia
Melianthus major	Melianthaceae	Shrub	F	AT, G	Australia, NZ
Monopsis debilis	Lobeliaceae	AH	Multi	F, Sk	Australia
Moraea fugax	Iridaceae	PH	Multi	F, Sk	Australia
Muraltia heisteria	Polygalaceae	Shrub	F		Australia
Nerine filifolia	Amaryllidaceae	PH	Multi		Australia, NZ
Ornithogalum thyrsoides	Hyacinthaceae	PH	F		Australia
Oxalis compressa	Oxalidaceae	PH	F		Australia
Oxalis flava	Oxalidaceae	PH	Multi	F, Sk	Australia
Oxalis glabra	Oxalidaceae	PH	F		Australia
Oxalis hirta	Oxalidaceae	PH	F		Australia, NZ, USA
Oxalis incarnata	Oxalidaceae	PH	F		Australia
Oxalis pes-caprae	Oxalidaceae	PH	Multi	F, Sk	Australia, Caribbean, Europe, NZ, USA
Pelargonium panduriforme	Geraniaceae	Shrub	F		NZ, USA
Pelargonium quercifolium	Geraniaceae	Shrub	F		NZ, USA
Pentaschistis pallida	Poaceae	PG	F	AT, G	Australia
Plectranthus ecklonii	Lamiaceae	Shrub	Multi	S	NZ
Plumbago auriculata	Plumbagnaceae	Shrub	Multi	AT, G, S	Australia, Canary Islands, Galapagos, Hawaii, USA
Psoralea pinnata	Fabaceae	Shrub	Multi	AT, F, G, S	NZ
Romulea rosea	Iridaceae	PH	F		Australia, NZ, USA

(Continued)

Table A1. (Contd.)

Taxon	Family	Life form	Main biomes	Details for multi	Invaded countries/regions
Ruschia caroli	Aizoaceae	Succ	Multi	F, Sk	Europe
Senecio elegans	Asteraceae	AH	F	AT, Sk	Australia, Europe, USA
Senecio glastifolius	Asteraceae	Shrub	F		Australia, NZ
Senecio macroglossus	Asteraceae	Succ	Multi		Australia, Galapagos, NZ
Solanum linnaeanum	Solanaceae	Shrub	Multi	AT, F, G	Australia
Sparaxis bulbifera	Iridaceae	PH	F		Australia
Sparaxis grandiflora	Iridaceae	PH	F		Australia, USA
Trachyandra divaricata	Asphodelaceae	PH	F		Australia
Tritonia crocata	Iridaceae	PH	F		Australia
Tritonia lineata	Iridaceae	PH	Multi	AT, G	Australia
Vellereophyton dealbatum	Asteraceae	AH	Multi	F, Nk, G, Sk	Australia
Wachendorfia thyrsiflora	Haemodoraceae	PH	F		NZ
Wahlenbergia capensis	Campanulaceae	AH	F		Australia
Watsonia borbonica	Iridaceae	PH	F		Australia
Watsonia marginata	Iridaceae	PH	F		Australia, USA
Watsonia meriana	Iridaceae	PH	F	G, Sk	Australia, NZ
Zaluzianskya divaricata	Scrophulariaceae	AH	F		Australia
Zantedeschia aethiopica	Araceae	PH	Multi	AT, F, G, S	Australia, NZ, USA

Life form: AH, annual herb; PH, perennial herb; AG, annual grass; PG, perennial grass; Succ, succulent.
Biomes: AT, Albany thicket; F, fynbos; G, grassland; Nk, Nama-karoo; S, savanna; Sk, succulent karoo.
Invaded countries: NZ, New Zealand.