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BIODIVERSITY RESEARCH

Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climatic suitability

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ABSTRACT

Most national or regional initiatives aimed at managing biological invasions lack objective protocols for prioritizing invasive species and areas based on likely future dimensions of spread. South Africa has one of the most ambitious national programmes for managing plant invasions in the world. There is, however, no protocol for assessing the likely future spread patterns needed to inform medium- to long-term planning. This paper presents an assessment of the climatic correlates of distribution of 71 important invasive alien plants, and an analysis of the implications of these findings for future invasions in different vegetation types in South Africa, Lesotho and Swaziland over the next few decades. We used a variant of climatic envelope models (CEMs) based on the Mahalanobis distance to derive climatic suitability surfaces for each species. CEMs were developed using the first three principal components derived from an analysis of seven climatic variables. Most species are currently confined to 10% or less of the region, but could potentially invade up to 40%. Depending on the species, between 2% and 79% of the region is climatically suitable for species to invade, and some areas were suitable for up to 45 plant invaders. Over one third of the modelled species have limited potential to substantially expand their distribution. About 20% of the vegetation types have low invasion potential where fewer than five species can invade, and about 10% have high invasion potential, being potentially suitable for more than 25 of the plant invaders. Our results suggest that management of the invasive plant species that are currently most widespread should focus on reducing densities, for example through biological control programmes, rather than controlling range expansions. We also identify areas of the region that may require additional management focus in the future.

Keywords

Bioclimatic modelling, biological invasions, Mahalanobis distance, predictive models, spatial distribution, Working for Water programme.

INTRODUCTION

Biological invasions are a major threat to biodiversity and ecosystem functioning worldwide (Mack *et al*., 2001). Many important management initiatives have been initiated in different parts of the world, particularly in the last two decades. Such programmes target invasions in many different ways and focus at spatial scales ranging from global, through national and regional, to local (Wittenberg & Cock, 2001). This paper addresses the need for better information to inform national policy on the management of alien plant invasions in South Africa.

South Africa has been invaded by many species with well-documented ecological and economic impacts (Richardson *et al*., 1997; Versfeld *et al*., 1998; Le Maitre *et al*., 2000; Richardson & van Wilgen, 2004; Van Wilgen, 2004). The country has a long history of research on, and management of, biological invasions, especially relating to invasive alien plants (Macdonald *et al*., 1986). A milestone in the management of alien plant invasions in South Africa was the initiation in 1995 of the national-scale Working for Water Programme (Van Wilgen *et al*., 1996; Van Wilgen *et al*., 1998; Van Wilgen, 2004). This programme has been widely lauded for its success in merging social, political, economic and environmental considerations (e.g. Hobbs, 2004). One of its biggest achievements has been the coordination of previously separate management initiatives (Van Wilgen, 2004). Despite its successes on many fronts, many challenges still confront the programme (Macdonald, 2004). One of these is the need to prioritize areas and species to maximize the cost effectiveness of control operations.

Systematic medium-term planning for a programme such as Working for Water that deals with many invasive species over a very large area demands an objective assessment of priorities for both species and areas. As a first step in this process, a classification of invasive alien plant species into major and emerging invaders for South Africa, Lesotho and Swaziland was recently proposed (Nel *et al*., 2004). This study highlighted the need for management to consider three categories of invaders: those species that are already widespread and abundant in the country, those that have only recently started to invade, and those that have not yet shown any sign of invasiveness or that are not yet present in the country but could pose a threat if introduced. Work is currently underway to improve our understanding of the extent of invasion (Versfeld *et al*., 1998) and dynamics (Robertson *et al*., 2003; Nel *et al*., 2004; Olckers, 2004; Robertson *et al*., 2004) of species in all these categories.

In this paper we present an approach for exploring the potential of important plant invaders to invade new areas in the region (South Africa, Lesotho and Swaziland). The analysis is based on a broad-brush assessment of climatic similarity between areas currently invaded and those not yet invaded. Many techniques have been proposed for understanding and modelling species-environment relationships (Franklin, 1995; Guisan & Zimmermann, 2000). Climate envelope models (CEMs), one type of predictive model, generate maps of potential species distribution using climatic characteristics where the species occurs. Major advantages of CEMs are their ability to cope with 'presence only' data, and their simplicity. Due to the relatively large number of plant invaders, a simple modelling technique, applicable to different taxa with a wide range of environmental requirements, was required, and CEMs were considered to be appropriate. The objectives of this study were to (a) develop climatic envelopes for major plant invaders; (b) map invasion potential for the whole country; and (c) assess the invasion potential of the region's vegetation types.

METHODS

Selecting invasive alien plant species

The Southern African Plant Invaders Atlas (SAPIA) is the best source of data on the distribution of invasive alien plants in South Africa, Lesotho and Swaziland. The SAPIA database contains records for over 500 species with information on their distribution, abundance, habitat preferences, and time of introduction (Henderson, 1998, 1999, 2001). Records are geo-referenced based on a quarter-degree grid system (hereafter quarter-degree squares or 'QDS', 15′ latitude × 15′ longitude, representing roughly 25 × 27 km). Nel *et al.* (2004) used species distribution and abundance data from SAPIA to identify 126 major plant invaders — species recorded as either widespread, or localized but abundant. Our analyses focused only on those major plant invaders with at least 50 records in SAPIA. Aquatic species were also excluded because their distribution is determined more by water availability than by climatic factors. The 71 major plant invaders selected for study are listed in Appendix S1.

Environmental modelling

Modelling the potential distribution of invasive species is always subject to uncertainties. For instance, the role of climate in controlling distribution is not the same for all species, and other factors such as disturbance regimes and biotic interactions may override climatic factors (Richardson & Bond, 1991; Hulme, 2003). Furthermore, the distribution of invasive species might not be in equilibrium with the environment because the geographical range of the species might still be expanding. Importantly, the majority of the species selected for study (Appendix S1) were introduced more than 100 years ago, allowing them time to sample a wide range of available habitats. An important assumption of our study is thus that the current distribution of the species in the region provides a good indication of their potential range in the region. We realize that potential distributions for some species (those for which human-aided dissemination has not afforded them opportunity to sample all potentially invasible habitats) may be underestimated. Similarly, for those species that have a scattered distribution over a large part of the region and/or where distribution is associated with human-induced disturbance more than inherent features of the environment, the potential distribution based on our assessments of climatic conditions is probably overestimated.

Despite these limitations, CEMs are very useful at a broad scale to develop a general picture of where species are most likely to invade, especially in this region with marked climatic gradients. For example, the mean annual rainfall exceeds 500 mm in the southern and eastern parts of the region but is less than 250 mm in the north-west and central interior (Schulze *et al*., 1997). Likewise, growing conditions in the interior are strongly influenced by cold winters and a higher frequency of frost than in coastal areas. Previous studies have also shown that, at the scale of the whole region, climatic factors were the best environmental variables for predicting the distribution of two important invaders in South Africa (Rouget & Richardson, 2003).

The predictive ability of CEMs, however, is highly dependent on the choice of climatic factors. We investigated the use of a range of climatic variables developed by Schulze *et al.* (1997). Preliminary analyses suggested that the relative importance of climatic factors was species-specific, making it difficult to identify a few 'generic' climatic variables, which could be applied for all our species. We therefore reduced the large number of possible explanatory variables to three components (principal component axes 1, 2 and 3) using Principal Component Analysis (PCA, Mardia *et al.*, 1979). The first three components of the resulting PCA explained over 95% of the initial variation, based on the seven climatic variables with the greatest influence on plant species distribution (see Table 1; Fig. 1). We then used these three climatic indices to derive the CEMs.

Most CEMs have used a rectilinear envelope based on minima and maxima of each climatic factor considered, and assign

Table 1 Results of principal component analysis. More than 95% of the variation of the original seven climatic variables was explained by three climatic components. The correlation between climatic variables and principal components is indicated and the two most correlated variables are shown in bold for each component. Climatic data are from Schulze et al. (1997)

Climatic variables	I component	II component	III component
Growth days per year	**0.53**	0.07	0.25
Minimum soil water stress	**−0.49**	−0.04	0.22
Frost duration	−0.11	**−0.60**	0.25
Growth temperature	−0.22	0.42	**0.64**
Mean temperature of the hottest month	−0.40	0.39	0.10
Mean temperature of the coldest month	0.17	**0.55**	−0.38
Mean annual precipitation	0.48	0.08	**0.51**

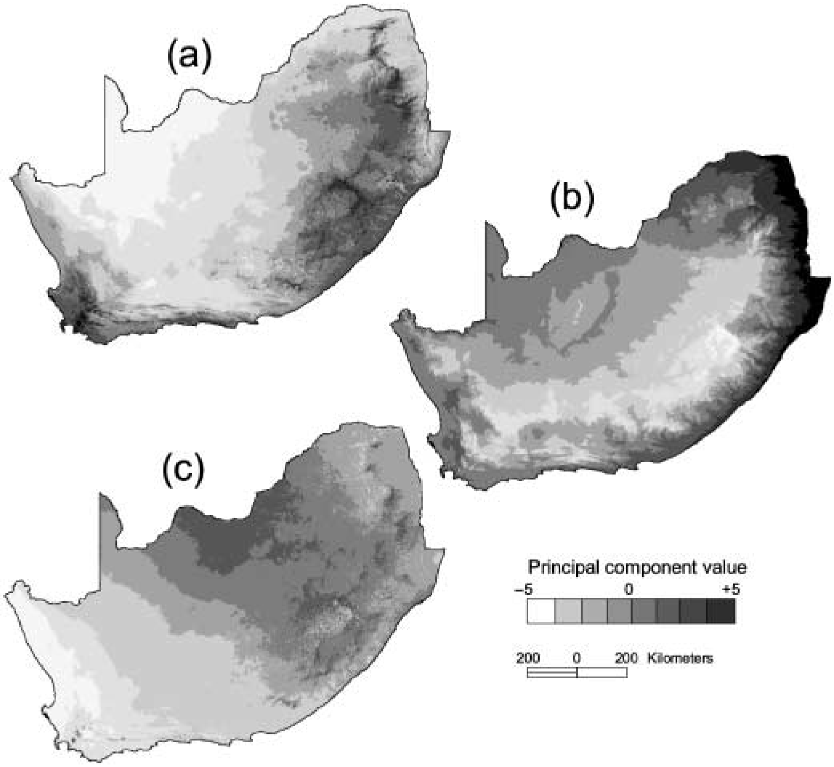

Figure 1 Climatic indices used to derive climatic envelope models. These were derived from Principal Component Analysis using seven climatic variables (see Table 1) and explained more than 95% of the initial variance. The first component (a) is mostly associated with growth days and minimum soil water stress; the second component (b) with frost duration and mean temperature of the coldest month, and the third component (c) with growth temperature and mean annual precipitation.

equal climatic suitability within the boundaries of the climatic envelope (Austin *et al.*, 1990; Busby, 1991). In this study, we used a variant of CEMs based on an oblique ellipse model, which calculates the Mahalanobis distance to the 'optimal' climate conditions (Farber & Kadmon, 2003). Niche theory supports the use of such models because they assume the existence of optimal environmental conditions for a species and that any deviation from this optimum is associated with a lower climatic suitability. These models are an improvement on traditional CEMs in that a continuous range of climatic suitability values can be equated with probability of occurrence.

For each species, the following procedure was followed. We extracted the QDS records where the species occurs, and determined the climate characteristics of each QDS based on the three principal components. As climatic data were available at a finer resolution (1 minute) than the species distribution data (15 min), we used the mean value of the principal components for each of the 225 cells within the QDS. We followed the approach by Farber & Kadmon (2003) and calculated the mean vector (m) of the three principal components, which represents the 'optimum' climatic condition. We also calculated the covariance matrix (**C**) from a matrix whose rows represent the QDS where the species was recorded and whose columns represent the corresponding values of the three principal components. Next, each 1-minute cell was assigned a Mahalanobis distance using m and **C**, defined as:

$$d^2 = (x - m)^T \mathbf{C}^{-1} (x - m)$$

where x represents the set of climatic conditions in each 1-minute cell, and d is the Mahalanobis distance from which we derived a climatic suitability index (see below).

Mapping potential range

The Mahalanobis distance (d) ranges from 0 to infinity, with 0 representing the optimum condition (in our case, the optimum climatic condition). Cells with a Mahalanobis distance less than 2.5 were considered climatically suitable. Although Farber & Kadmon (2003) chose a higher cut-off ($d = 4$), preliminary analysis suggested that a cut-off of 2.5 provides the most accurate climatic envelopes. Expert assessment also found that envelopes including d-values greater than 2.5 were unrealistic for species whose climatic envelopes were well understood. We rescaled the d-values to obtain a climatic suitability index ranging from 0 to 100, where 0 represents any value of d greater than 5, 50 represents $d = 2.5$ and 100, $d = 0$. We assumed that alien plant species would have the potential of spreading in areas identified as the most climatically suitable (i.e. greater than 50). For riparian species, we only modelled climatic suitability within those 1-minute cells containing sections of perennial or non-perennial rivers (24% of the region) based on the national 1: 500,000 scale river database.

For each species, we calculated the percentage of the region's area that is climatically suitable for that species, as well as the increase in area relative to its current distribution. For riparian species, this was calculated in relation to the total area of riparian habitat. The current distribution of the 71 modelled species was compared to the potential range. Relative increase was calculated as the difference between potential and current range, divided by the current range. Finally, we summarized invasion potential by calculating the total number of plant invaders that could potentially occur in each 1-minute cell based on climatic suitability, and the average climatic suitability for those species.

Unfortunately, no other independent data set was available for testing model predictions of the 71 species. For each species, we generated a random QDS set of pseudo-absences (with sample size equivalent to the number of QDS where the species was recorded present). We used pseudo-absence and presence records to calculate presence accuracy (% of QDS, where the species occurs, correctly classified by the CEM), absence accuracy (% of QDS, where the species is supposed absent, correctly classified by the CEM), and the Kappa statistic. Kappa statistic evaluates the predictive model accuracy relative to the accuracy that might have resulted by chance (Cohen, 1960; Fielding & Bell, 1997). It ranges from — 1 (complete disagreement) to 1 (perfect agreement) with 0 indicating random agreement. Model accuracy (i.e. high Kappa value) should be greater for species at equilibrium with the environment. We assumed that species introduced long time ago would have reached pseudo-equilibrium and analysed the Kappa values in relation to the introduction date of the species.

Prioritizing vegetation types

We used the vegetation map of South Africa, Lesotho and Swaziland (Mucina & Rutherford, 2005) to assess invasion potential of the nine biomes and the 441 vegetation types defined for the region. Vegetation types are ecological units, which reflect similarities in climate and soils, and in processes, for example, disturbance regimes such as fires (Mucina & Rutherford, 2005). This suggests that we can treat them as homogenous units in terms of their susceptibility to invasion by different species. For each alien plant species, we selected areas of highest climatic suitability (i.e. greater than 50). We then calculated the median number of potential plant invaders per 1-minute cell for each biome and vegetation type. The average climatic suitability per 1-minute cell was summarized for each vegetation type. Based on natural breaks in the frequency distribution of the median number of potential plant invaders per vegetation type, we identified four categories which describe the invasion potential of vegetation types in the region.

RESULTS

Potential distribution

Climate envelope models (CEMs) appear very suitable for providing a broad picture of the potential spread of major plant invaders in the region. The Kappa statistic was 0.6 on average for all species and greater than 0.5 for 52 species (Appendix S1). On average, 80% of the QDS where each species currently occurs were identified as climatically suitable for that species (Appendix S1). The climatic envelopes for three species selected as representative of different types of distribution in the region also match their current distribution reasonably well (Fig. 2).

Major plant invaders currently occupy between 1% (*Casuarina equisetifolia*) and 43% (*Opuntia ficus-indica*) of the QDS in the region. The CEMs show that, depending on the species, between 2% (*Casuarina equisetifolia*) and 79% (*Arundo donax*) of the region is potentially suitable for species to invade. Most of the species are currently confined to 10% or less of the region, but could potentially invade up to 40%. Based on climatic suitability, only 14 species have the potential to invade more than 50% of the country (Appendix S1). Of these, five species only invade landscapes (i.e. non-riparian areas), but all of these were either cacti (*Opuntia* spp.) or sisals (*Agave* spp.), which can invade large areas of the arid and semiarid interior. Three of the 14 species are strictly riparian invaders (*Arundo donax*, *Eucalyptus camaldulensis*, *Nicotiana glauca*), and six invade both landscape and riparian habitats. Our results suggest that more than a third of the major plant invaders have limited potential to substantially increase their range (where the potential distribution is at best twice that of the current extent). The proportional increase in potential distribution exceeds 1000% for seven species (Appendix S1). There was a negative relationship between current distribution and model accuracy (based on Kappa statistic). Model accuracy tended to be higher for species with small distribution than for widespread species (Fig. 3a). However, there was no relationship between time since introduction and model accuracy (Fig. 3b).

CEMs predicted that some parts of the region were climatically suitable for up to 45 major plant invaders (Fig. 4a). Over half of the region is suitable for between one and 15 major plant invaders, and only 2% of the region was predicted to be climatically unsuitable for invasion by any of the major plant invaders.

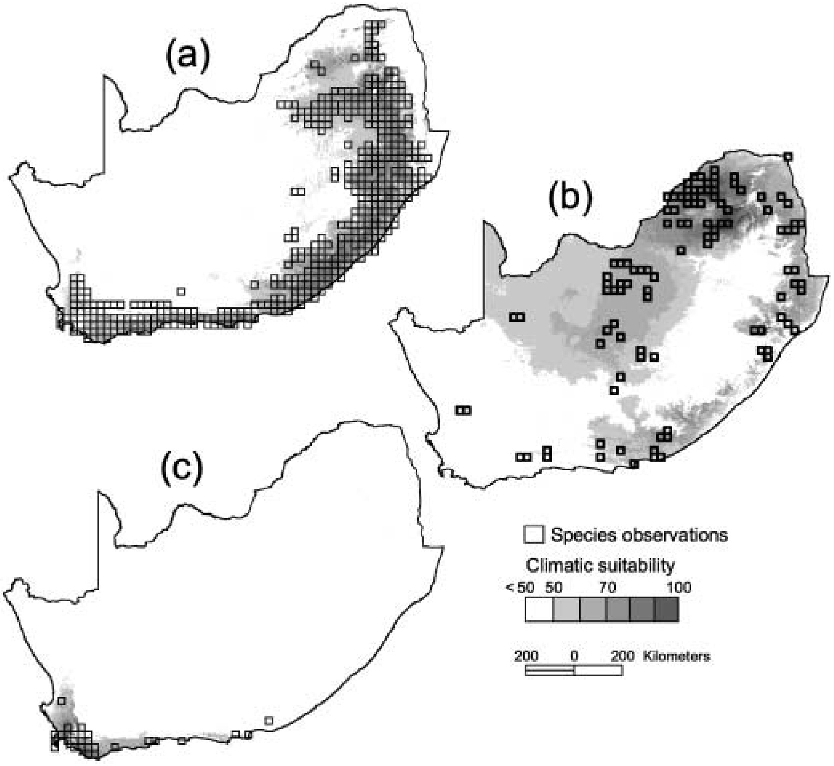

Figure 2 Species presence observations and climatic suitability derived from climatic envelope models for three characteristic species in South Africa, Lesotho and Swaziland: (a) *Acacia mearnsii*, a very widespread and abundant invader; (b) *Opuntia stricta*, a widespread and common invader; and (c) *Hakea drupacea*, a localized and abundant invader.

The eastern coastal plain and the north-eastern interior are climatically suitable for most of the currently invading species (Fig. 4a). However, average climate suitability varies within these areas. For example, although fewer species can invade the Agulhas Plain at the southernmost tip of the region, the average climatic suitability for those species is much higher than for parts of the Eastern Cape where more species could invade (Fig. 4b). The low potential number of invaders and average climatic suitability of the escarpment, Drakensberg and mountains of the Western Cape (Fig. 4a and b) appears to be primarily due to frequent frosts and low mean temperatures of the coldest month (second principal component, Fig. 1b, Table 1) rather than rainfall or otherwise favourable growing conditions.

Invasion potential of biomes and vegetation types

Vegetation types and biomes differ markedly in their potential for invasion by the suite of major plant invaders explored in this study. Relatively few alien plant species can invade the desert and succulent karoo biomes, whereas more than 15 species could potentially invade the Albany thicket, forest and grassland biomes (Table 2). The maximum potential number of major

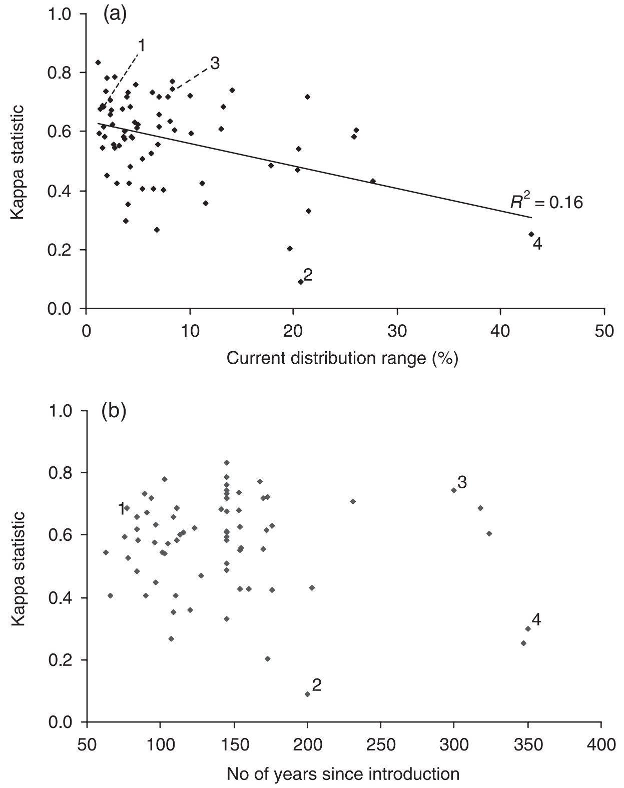

Figure 3 (a) Relationship between current geographical range and model accuracy (Kappa statistics) based on climatic envelopes models for 71 major plant invaders in South Africa, Lesotho and Swaziland. Kappa statistics range from 0 (random agreement) to 1 (perfect agreement. Current distribution was derived from the SAPIA databases based on the QDS where the species was recorded (expressed as a percentage of the region). (b) Relationship between time since introduction and model accuracy (Kappa statistic). Numbers indicate a few representative species: (1) *Schinus terebinthifolius*; (2) *Arundo donax*; (3) *Psidium guajava*; and (4) *Opuntia ficus-indica*.

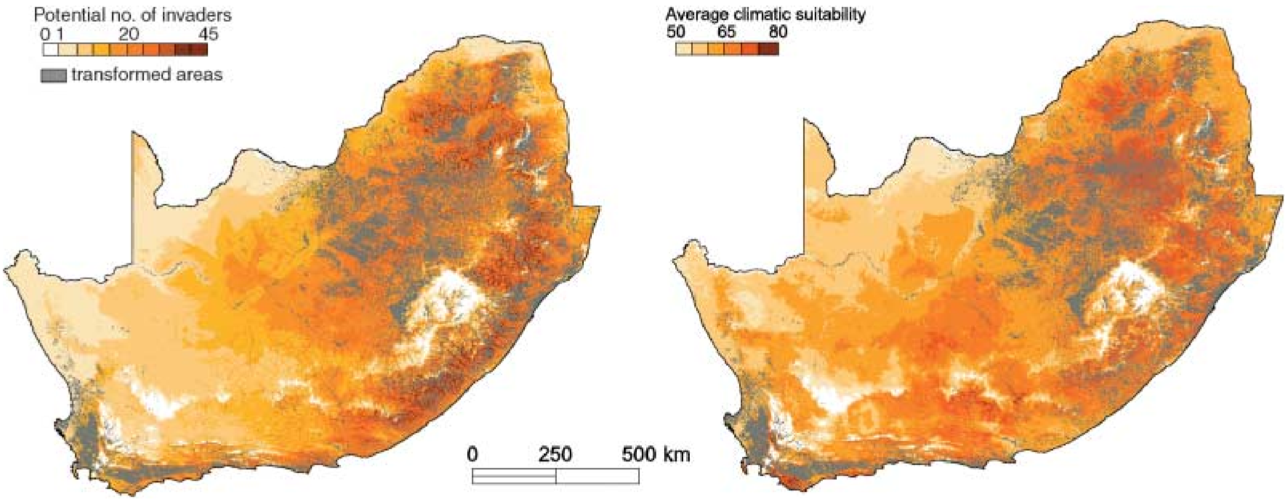

Figure 4 Potential number of major plant invaders and their average climatic suitability based on climatic envelope models.

Table 2 Invasion potential summarized in major biomes and habitats (*sensu* Mucina & Rutherford, 2005). The median number, as well as the range, of plant invaders for which the climatic conditions are suitable is indicated (no. invaders)

Biome/Habitats	no. invaders
Biomes	
Albany Thicket	19 (1–31)
Desert	2 (0–15)
Forest	17 (0–42)
Fynbos	11 (0–36)
Grassland	20 (0–45)
Nama-Karoo	10 (0–34)
Savanna	15 (0–44)
Succulent Karoo	5 (0–26)
Wetland habitats	10 (0–42)

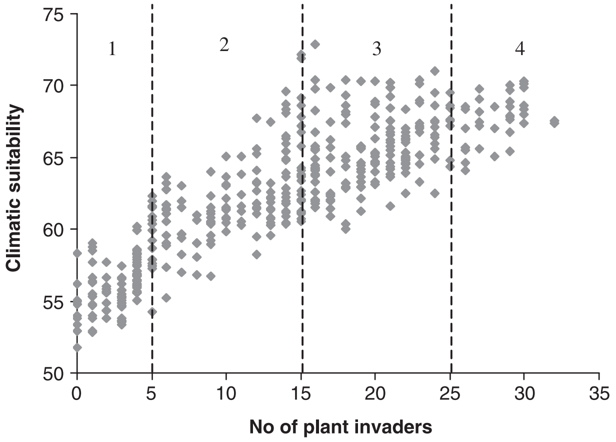

Figure 5 Relationships between average climatic suitability and potential number of major plant invaders for 441 vegetation types of South Africa, Lesotho and Swaziland. Predictions were based on climatic envelope models. Four categories (labelled 1–4 on the figure) were identified based on natural breaks in the frequency distribution of the median number of potential invaders per vegetation type.

plant invaders is relatively similar in all biomes, except for the desert and succulent karoo, which are suitable for fewer species. The average climatic suitability is however, fairly similar among biomes (Table 2).

The average climate suitability and the number of potential plant invaders per vegetation type are positively correlated (Fig. 5). In other words, areas of high climatic suitability are also suitable for many species. There is a direct relationship between climatic suitability and the number of potential invaders up to an average climatic suitability of around 65%. Thereafter, there seems to be very little relationship, indicating that climatic factors are important, but only below certain threshold values. Figure 6 shows the invasion potential for each vegetation type, classified into four categories based on the potential number of plant invaders. Just over 20% of the region's vegetation types are characterized by very low invasion potential where less than 5 species could invade (Fig. 6); most of this area falls within the desert and succulent karoo biomes. The second group, characterized by low invasion potential (5–15 potential plant invaders), comprises mainly fynbos, succulent karoo and savanna types, the third group (5–25 potential plant invaders) mainly fynbos and grassland types, and the fourth group (more than 25 potential plant invaders), comprising about 10% of vegetation types (44). Vegetation types in group 4 occur mainly on the eastern coastal plains (such as Midlands mistbelt grasslands) and in the northern part of the country (mostly savanna types).

DISCUSSION

Modelling approach

The variant of CEM used in this study allowed us to express potential distribution as continuous gradients at a 1-minute

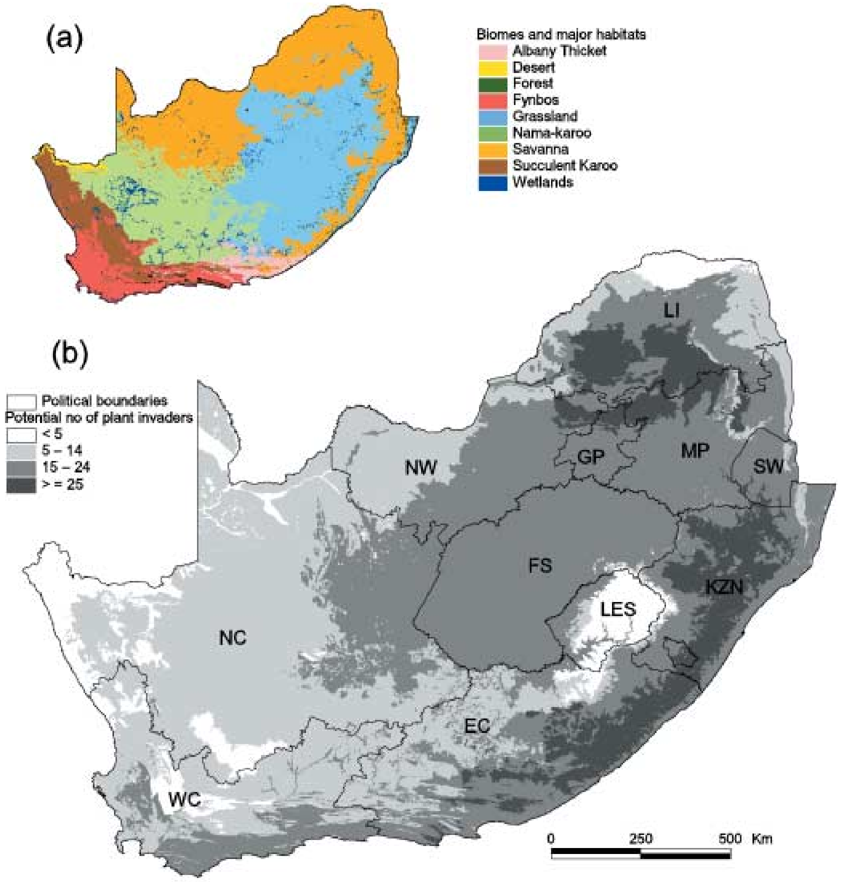

Figure 6 South African biomes and major habitats (a), and invasion potential of vegetation types based on the potential number of major plant invaders (b). Four categories were identified: (1) < 5 potential invaders; (2) 6–15 potential invaders; (3) 16–25 potential invaders; and (4) > 25 potential invaders. South African provincial boundaries, and Lesotho and Swaziland borders are indicated: WC = Western Cape; NC = Northern Cape; EC = Eastern Cape; KZN = KwaZulu-Natal; MP = Mpumalanga; LI = Limpopo; GP = Gauteng; NW = North-west; FS = Free State; LES = Lesotho; and SW = Swaziland.

spatial resolution rather than discrete values for quarter-degree squares. Although downscaling the resolution of data can introduce more uncertainty (Araujo *et al*., 2004), this facilitated an analysis of invasion potential of biomes and vegetation types. Such an analysis could not be done using the QDS data from SAPIA, since many QDS contain more than one biome or vegetation type.

The major limitation for modelling invasive species is the assumption that species are at equilibrium with the environment. Although, most of the species modelled here have a sufficiently long history in the region to have sampled most of the environmental conditions, their distribution is probably not yet at equilibrium. Furthermore, current model accuracy techniques (such as Kappa) might not be appropriate for modelling invasive species. Low model accuracy (i.e. low Kappa values) could mean either that the climatic envelope does not capture the environmental determinants of the species distribution, or that the climate envelope is correct and the species has huge potential for spreading into suitable environment.

Three main factors are likely to affect the accuracy of our results. Most importantly, CEMs assume the current distribution of the species provides a good indication of their potential range. Where this is not the case, potential range will be over- or underestimated. Potential range is likely to be overestimated for species occurring in few scattered locations throughout the entire region, but underestimated for species currently occurring in a small, clumped range. Secondly, spatial bias in the SAPIA database (see Nel *et al*., 2004 for discussion) may have led to underestimation of the current and potential distribution of species that are less conspicuous and/or that are under-represented in the database for other reasons (e.g. difficult to identify to species level). Lastly, the process of averaging the climatic suitability values (based on the principal component scores) of the 225 1-minute cells per QDS assumes that the mean values represent the location where the species occurs. The likelihood of there being a significant error in this assumption depends on the variability of the climatic factors in the QDS, and will be greater in areas of complex topography. At the broad scale at which this analysis is intended to inform management and planning, we do not believe that any of these factors have a substantial effect on the overall accuracy or usefulness of the results. More detailed assessments will, however, be necessary for local decision making.

Potential spread of major and emerging plant invaders

Our study focused on the major plant invaders identified by Nel *et al*. (2004), because they are the invasive species most likely to be problematic in the medium term, and management of these species will use most of the available resources. There was also sufficient data on current distribution of major plant invaders within the region for us to have reasonable confidence in the potential distributions we generated. Clearly, emerging invaders (not covered in this study) must also receive attention in long-term planning, as it is well known that control options are most cost effective at the early stages of invasion (Hobbs & Humphries, 1995; Myers *et al.*, 2000; Olckers, 2004). Prioritization for these species requires a different approach to that adopted in this study.

Results show that some of the regions' worst perceived invaders (Le Maitre *et al.*, 2000; Robertson *et al.*, 2003), such as *Acacia mearnsii*, *A. saligna*, *Chromolaena odorata*, *Lantana camara*, and *Opuntia ficus-indica*, have much less potential to substantially increase their ranges than many other species (Appendix S1). This suggests that that management of these species should focus on preventing increased density within their current range, thus averting escalating impacts. The species that have the greatest potential to increase are not those that have previously been identified by experts as important invaders (Robertson *et al.*, 2004). Only three species (*Eucalyptus camaldulensis*, *Pinus elliottii* and *P. halepensis*) out of the 10 with the greatest potential increase occur on the expert-generated list of Robertson *et al.* (2004), and none of these were in their top 10. As these species could potentially have major impacts in the near future, more work is needed on their distribution and determinants of spread (including climatic requirements).

Spatial pattern and invasion potential of vegetation types

The map of potential number of major plant invaders in the region (Fig. 4a) is generally similar to the current distribution patterns (Nel *et al.*, 2004), although the Free State and Northwest provinces of South Africa could potentially be invaded by many more species than currently occur in these areas. The potential number of invaders in the mountains of the Western Cape (Fig. 4a) is also surprisingly low, given the current numbers of major plant invaders. Mountain fynbos is one of the most severely impacted habitats in the region (Richardson *et al.*, 1997), but has only been heavily invaded by a small number of tree and shrub species that are preadapted to the nutrient-poor soils and fire regime (Richardson & Cowling, 1992). These habitats are not suitable for invasion by most of the species in Appendix S1.

Invasion potential differs substantially among vegetation types. The fynbos lowlands, and parts of the grassland, savanna and thicket biomes are highly suitable (climatically) for invasion by a wide range of species (Fig. 4a,b). From a watershed perspective, the susceptibility of the grasslands to further invasions, particularly by woody species, is of concern because watersheds in this region have relatively high water yields and woody plant invasions can significantly reduce runoff (Le Maitre *et al.*, 2000). Only a few areas appear to be suitable for more than 25 species. These areas do not always coincide with areas where management programmes are focusing their efforts. For example, about a third of the expenditure of the Working for Water Programme has been in the fynbos areas of the Western and Eastern Cape provinces (Marais *et al.*, 2004), which have a lower invasion potential (i.e. are potentially suitable for fewer major invasive species). As discussed above, this area is severely affected by a few ecosystem-transforming invasive species (Richardson *et al.*, 1997) and substantial management intervention is clearly justified. We have identified areas that are highly suitable for invasion by a wide range of species. Clearly, the potential number of invaders and average climatic suitability are not the only, or even the most important, indicator of the impacts invading species can have. Impact is defined as the product of a species' range, abundance and per capita effect (Parker *et al.*, 1999; Richardson & van Wilgen, 2004). Finer-scale prioritization will need to include an assessment of the impact.

In conclusion, most of the major invaders have limited potential to expand their distribution (at least under current climatic conditions), and management should seek to control density rather than to prevent range expansions. This strongly supports the use of biological control which is very effective at maintaining invaders at low densities (Olckers, 2004). Our analyses have also identified parts of the region where management of range expansions could be important, notably in the Transkei region of the Eastern Cape, in northern KwaZulu-Natal, and the bushveld areas of Gauteng and Limpopo (Fig. 6).

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SUPPLEMENTARY MATERIAL

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Appendix S1. Characteristics of major plant invaders modelled using climatic envelope models (CEMs). Categories follow Nel *et al.* (2004). Current distribution was derived from the SAPIA databases based on the QDS (expressed as a percentage of South Africa, Lesotho and Swaziland) where the species was recorded. The area climatically suitable was derived from CEMs using three principal components of a climatic analysis of the region. The increase was calculated as the difference between potential and current range, divided by the current range. Accuracy was calculated using (a) the Kappa statistic (b) the percentage of QDS where the species occurs which were found to be climatically suitable (presence accuracy) (c) the percentage of QDS where the species does not occur which were not found to be climatically suitable (absence accuracy). The Kappa statistic evaluates the model accuracy relative to the accuracy that might have resulted by chance. It ranges from − 1 (complete disagreement) to 1 (perfect agreement) with 0 indicating random agreement.

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