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Impacts of climate change on invasive *Lantana camara* L. distribution in South Africa

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Climate change and invasive species are now seen as two major contributors to global biodiversity change. The combined effects of these two factors have serious implications for biodiversity and agriculture. *Lantana camara* L. (*sensu lato*) (lantana) is a woody shrub that is highly invasive in many countries of the world including South Africa where it has a profound impact on biodiversity, water resources and agriculture. Strategies to manage and control this highly noxious weed will benefit from information on its likely potential distribution under current and future climate. CLIMEX, a species distribution modelling software, was used to develop a process-oriented niche model to estimate its potential distribution under current and future climate scenarios. Model calibration was carried out with phenological observations and geographic distribution records of lantana. The potential distribution of lantana under current climate showed a good match to its current distribution in South Africa. Under future scenarios, the climatically suitable areas for lantana were projected to contract in the northern provinces of Limpopo and Mpumalanga as well as coastal areas of Western Cape Province. However, lantana's potential distribution may expand further inland into new areas in KwaZulu-Natal and Eastern Cape provinces. The results suggest that lantana management initiatives in areas where climatic suitability is likely to decline should focus on controlling the density of invasion rather than curbing range expansion. On the other hand, areas where climatic suitability is projected to increase will require ongoing monitoring to prevent further range expansions.

Key words: CLIMEX, niche models, species distribution models, biotic invasions, weeds, climate change.

INTRODUCTION

The major reason for many deliberate introductions of non-native species throughout the world has been for the provision of benefits to human societies. Food, shelter and aesthetic enjoyment are included among these benefits. However, many of these introduced species have become invasive in natural as well as agricultural ecosystems (Groves et al., 2001). An invasive species is broadly defined as an introduced species that becomes established and spreads outside its native range (Jeschke and Strayer, 2005). Biological invasions have been the focus of much attention and research because it has led to increasing biotic homogenization of the Earth's

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flora and fauna (Hobbs, 2000; Mooney and Hobbs, 2000). The main impacts of invasive species are a global loss of biodiversity (Czech and Krausman, 1997; Dirzo and Raven, 2003) and alteration of ecosystem structure and function (Binggeli, 1996; Vitousek et al., 1997; Sutherst, 2000). Plant invaders, in particular, can impact native ecosystems through changes in fire regime, nutrient cycling, hydrology and energy budgets, thus causing a reduction in the abundance or survival of native species (Mack et al., 2000). The economic costs associated with biological invasions are also substantial due to lost yields and control efforts, particularly in agriculture (Vitousek et al., 1997). Furthermore, based on the overwhelming evidence for rapid climate change effects (IPCC, 2007), it is essential to consider the influence of climate change on the rate and extent of biological invasions (Walther et al., 2009). The immediate effect of climate change on invasive species will most likely be shifts in their distributions facilitated by changes in temperature and rainfall patterns that define their range boundaries. Climate change may favour species that can tolerate a wide range of climatic conditions and thus such species may have greater competitive success than most native species (Walther et al., 2009; Sutherst et al., 2007a).

Lantana camara L. (*sensu lato*) (lantana) is an invasive species that has had substantial negative impacts in many tropical and subtropical countries outside its native range of central and northern South America and the Caribbean. Sixty countries or island groups between 35°N and 35°S are included in its global distribution (Day et al., 2003). It has been ranked among the world's worst 100 invasive alien species (Lowe et al., 2000) while Sharma et al. (2005) considered it as one of the world's ten worst weeds. Its major impacts include a reduction in native species diversity, local extinctions, decline in soil fertility and allelopathic alteration of soil properties as well as an alteration of ecosystem processes (Day et al., 2003). It was introduced into South Africa in the mid 1800s for horticultural purposes (Richardson et al., 1997; Day and Neser, 1999) and due to its ability to hybridize easily with other entities, there are now reportedly up to 40 varieties in this country (Graaf, 1986). Lantana has been classified as a widespread species that has invaded many biomes including forest, savannah, fynbos, Indian Ocean coastal belt and grassland with the species being particularly prominent in the savannah and Indian Ocean coastal belt biomes (Vardien et al., 2012). Various studies have identified lantana as a major invader in South Africa (Richardson et al., 1997; Robertson et al., 2003; Nel et al., 2004), with over 2 million hectares invaded by this species (Le Maitre et al., 2000). Lantana is also listed as a category one weed (prohibited weeds that must be controlled in all situations) in the Conservation of Agricultural Resources Act. Furthermore, in an assessment of the potential impacts of plant invaders on biodiversity, water resources and rangeland productivity in South Africa, lantana scored the highest in terms of its impacts on biodiversity (Le Maitre et al., 2004). It also has a large impact on water resources by using up to 97.14 m^3 of the surface water resources (Le Maitre et al., 2000). This species has also been the subject of the most intensive biological control programme in South Africa (Richardson et al., 1997; Urban et al., 2011). In the last 23 years, 30 possible biological control agents have been evaluated and seven were found suitable for release into South Africa (Urban et al., 2011). However, only five of these have been established but they do not provide adequate control since they neither kill the lantana plants, nor stop the weed population increase (Day and Neser, 1999; Urban et al., 2011). The limited knowledge on the taxonomy of this species has made it difficult to select effective biological control agents and thus lantana is still not under adequate control and remains a problem in many areas of South Africa (Richardson et al., 1997; Urban et al., 2011).

Information on the expected potential distribution and relative abundance of this species under current and future climate scenarios is necessary for risk assessment and formulation of effective management strategies by biosecurity agencies in South Africa. Ecological niche models are useful tools in such instances (Peterson et al., 2011).

In simple terms, occurrence records of the target species in one region are used to calibrate the model and then projected onto other regions where the species may or may not currently be invasive (Peterson et al., 2011). Thus, the species' 'environmental envelope' or its preferred climate is inferred from its occurrence data (Barry and Elith, 2006). One major assumption that underlies such models is that climate is the primary factor defining the potential range of plants and other poikilotherms (Woodward, 1987). A range of software is now available which can be used to model species' current and future distributions (Kriticos and Randall, 2001; Hirzel and LeLay, 2008) one of which, CLIMEX, has been widely used to assess invasion risks from invasive alien species (Kriticos et al., 2011a; Chejara et al., 2010; Kriticos and Leriche, 2010; Taylor et al., 2012a, b). It is a mechanistic model (Hijmans and Graham, 2006) which is well suited for applications that involve transferability or projections of species distribution into novel environments (Randin et al., 2006), such as investigating the impacts of climate change on species' potential ranges (Kriticos et al., 2011a).

So, the objectives of this study were (i) to use the CLIMEX modelling package to develop a model of the climate responses of lantana, and (ii) use this model to assess the impacts of climate change on its potential distribution in South Africa using two global climate models (GCM), CSIRO-Mk3.0 and MIROC-H based on the A1B and A2 SRES (Special Report on Emissions Scenarios) emission scenarios for 2030, 2070 and 2100.

MATERIALS AND METHODS

CLIMEX software

CLIMEX for Windows Version 3 (Hearne Scientific Software, 2007; Sutherst et al., 2007a) was employed in model development of the potential distribution of lantana under current and future climate scenarios. The basis of this software is an eco-physiological growth model which assumes that a population experiences a favourable season with positive growth and an unfavourable season with negative population growth. Geographic distribution data and phenological observations are used to infer parameters that describe a species' response to climate (Sutherst et al., 2007b). The parameters can then be applied to novel climates so that the potential distribution of a species in new regions or under climate change scenarios can be deduced (Kriticos et al., 2011a). The temperature (temperature index) and moisture (moisture index) requirements of a species are used to determine the potential for population growth during favourable climate conditions, termed the annual growth index (GI_A). The likelihood of survival during unfavourable conditions is described by four stress indices (cold, wet, hot and dry) and up to four interaction stresses (hot-dry, hot-wet, cold-dry and cold-wet). Weekly calculations of the growth and stress indices are combined into an overall annual index of climatic suitability, the ecoclimatic index (EI), which is theoretically scaled from 0 to 100. An EI value of zero indicates that the species will not be able to survive at that location, 1-10 indicate marginal habitats, 10-20 can support substantial populations while EI values >20 are highly favourable (Sutherst et al., 2007b). A detailed description of parameters is provided in Sutherst and Maywald (1985). The methodology described in Sutherst and Maywald (1985), Kriticos et al. (2011a) and Shabani et al. (2012) was used to fit the CLIMEX parameters for lantana.

Meteorological data and climate change scenarios

The CliMond 10´ gridded climate dataset (Kriticos et al., 2011b) was employed to carry out the modelling component of the study. In this dataset, historical climate (averaging period 1950-2000) is represented by five variables, average minimum monthly temperature (*T*min), average maximum monthly temperature (*T*max), average monthly precipitation (*P*total) and relative humidity at 09:00 h (*RH*09:00) and 15:00 h (*RH*15:00). Potential future climate in 2030, 2070 and 2100 is represented by the same five variables, based on the CSIRO-Mk3.0 and MIROC-H Global Climate Models (GCM) (Gordon et al., 2002) with the A1B and A2 SRES scenarios (IPCC, 2000). The A1B scenario depicts a balanced use of fossil and non-fossil resources in the future whereas the A2 scenario depicts a varied world with high population growth coupled with slow economic development and technological change. The major reason for not including the B family of scenarios in this study was based on the findings that recent global temperature increases were much higher than the hottest IPCC scenarios (Rahmstorf et al., 2007).

CLIMEX parameters

The Global Biodiversity Information Facility (GBIF) is a database of natural history collections around the world for various species and it is available for download. A total of 4126 records on the global distribution of lantana were downloaded from GBIF. However, only 1740 of these were used in parameter fitting and the others were discarded since many records did not have geolocations or were repetitions. Of these, 1139 were native and 601 were exotic records. Data on the alien distribution of lantana were also used for fitting stress parameters (SAPIA, 2006; Press et al., 2000; Chen and Gilbert, 1994; Thakur, 1992; Jafri, 1974; Biswas, 1934). Inclusion of native and alien distribution data in model parameterization ensured that the complete range of environmental conditions in which lantana may occur was covered. Seasonal phenology data from the southern states of Brazil (Winder, 1980, 1982) was used to fit growth parameters. Australia has extensive distribution data on lantana and this was reserved for model validation and thus not used in parameter fitting. Iterative adjustment of each parameter was conducted until a satisfactory match was obtained between the potential and known distribution of lantana in these areas, that is, to ensure that the maximum number of occurrence points fell within the modeled distribution. The aim was to achieve maximum EI values near known large and healthy populations and to minimize EI values outside the recorded distribution of lantana.

Stress parameters

The southern limits of lantana distribution in Argentina and northern limits in Nepal, Pakistan and China were defined by applying two cold stress mechanisms. The cold stress temperature threshold (TTCS) was set at 5°C with the frost stress accumulation rate (THCS) at -0.004/week based on the observation that lantana seldom occurs where temperatures frequently fall below 5°C (Cilliers, 1983). Furthermore, the cold-stress degree-day threshold (DTCS) was set at 15°C days, with the stress accumulation rate (DHCS) set at -0.0022/week so that the potential distribution was restricted to the known southern limits in Buenos Aires and northern limits in India, Nepal and China. The heat stress parameter (TTHS) was set at the same level as the limiting high temperature (DV3), 33°C, with a stress accumulation rate (THHS) of 0.001/week. This setting allowed lantana to persist along the Western Ghats (Murali and Sidappa Setty, 2001) as well as in Bengal and Assam in India where it is reportedly common (Biswas, 1934). The dry stress parameter was set at the same level (0.1) as the lower soil moisture threshold (SM0) with the stress accumulation rate set at -0.01/week. This excluded the species from the drier western parts of South Africa where it survives only as an ornamental plant (Cilliers and Neser, 1991). The wet stress threshold (SMWS) was set to 1.6 and the accumulation rate (HWS) set at 0.01/week. These were fitted based on the observations that lantana can tolerate up to 3000 mm of rainfall per year as long as the soil is not waterlogged for prolonged periods (Day et al., 2003; Thaman, 1974). These settings allowed the species to grow well in Indonesia and the Philippines (Holm et al., 1991) as well as in central Burma, but excluded it from the wetter coastal areas (Biswas, 1934).

Growth parameters

The limiting low temperature (DV0) was set at 10°C based on Winder (1980) observation that 'cold winter temperatures caused cessation of growth with a substantial loss in leaves and side-branches'. This was based on seasonal phenology data from Iguazu (25°33´S, 54°34´W) in Brazil where winter temperatures can get as low as 8°C and also Stirton (1977) observation that in South Africa, lantana is found in areas with a mean annual surface temperature greater than 12.5°C. The 10°C value was chosen as a compromise between the South African distribution data and the phenology data from Iguazu. The limiting high temperature DV3 was set at 33°C based on summer temperatures in Iguazu which rarely exceed 33°C and where lantana grows rapidly during summer (Winder, 1980). The lower (DV1) and upper (DV2) optimal temperatures were set at 25 and 30°C, respectively, based on seasonal phenology at Iguazu, and these provided a good fit to the observed South American, Asian and South African distribution. The lower moisture threshold (SM0) was set at 0.1 which excluded

Table 1. The CLIMEX parameter values that were used for *Lantana camara* L; taken from Taylor et al. (2012a).

Parameter	Mnemonic	Value
Limiting low temperature	DV0	10°C
Lower optimal temperature	DV1	25°C
Upper optimal temperature	DV2	30°C
Limiting high temperature	DV3	33°C
Limiting low soil moisture	SM0	0.1
Lower optimal soil moisture	SM1	0.5
Upper optimal soil moisture	SM2	1.2
Limiting high soil moisture	SM3	1.6
Cold stress temperature threshold	TTCS	5°C
Cold stress temperature rate	THCS	-0.004 /week
Minimum degree-day cold stress threshold	DTCS	15°C days
Degree-day cold stress rate	DHCS	-0.0022 /week
Heat stress temperature threshold	TTHS	33°C
Heat stress temperature rate	THHS	0.001 /week
Dry stress threshold	SMDS	0.1
Dry stress rate	HDS	-0.01 /week
Wet stress threshold	SMWS	1.6
Wet stress rate	HWS	0.01 /week

lantana from the drier western parts of South Africa where it survives only as an ornamental (Cilliers and Neser, 1991). Lantana grows well during the months of January to March in Iguazu (Winder, 1980) and thus the lower (SM1) and upper (SM2) optimum moisture thresholds were set at 0.5 and 1.2, respectively, to improve species growth during these months. The upper soil moisture threshold (SM3) was set at 1.6 to permit growth in the Philippines and Indonesia where it has been reported as a troublesome weed (Holm et al., 1991). The parameters were checked to ensure that they were biologically rational (Table 1). They were then used to model potential lantana distribution in South Africa under the reference climate (averaging period 1950-2000) as well as climate change scenarios. For a more detailed explanation of the parameter-fitting procedure, refer to Taylor et al. (2012a, 2012b) and Taylor and Kumar (2012).

RESULTS

Historical climate

There is a good match between the current global distribution of lantana and the modelled global climatic suitability (Figure 1). The CLIMEX modelling shows that large parts of the tropics and subtropics have suitable climatic conditions for lantana. Most of the central, eastern and parts of western Africa as well as Madagascar show climatic suitability for this species. The southern states of USA, large parts of South and Central America and Asia are also projected to be climatically suitable. Although there is a good match between the current global distribution and the modelled global climate suitability, this does not account for the occurrence records from Mediterranean Europe because lantana is mostly grown as an ornamental plant in this region (Garibaldi et al., 2008). Furthermore, parts of Africa that have been projected as climatically suitable do not show many occurrence records because there is a chronic lack of data across much of Africa, where lantana is certainly present. Model validation was conducted using the distribution data for Australia as these records were not used for parameter fitting. The occurrence records match well with the modelled climate suitability for the continent (Figure 2), and the present Australian distribution is consistent with the Ecoclimatic Index. Approximately 87% of the occurrence records fall within the suitable and highly suitable categories.

The occurrence records (Figure 3) agree well with the modelled climate suitability (Figure 4) and the present South African distribution is consistent with the Ecoclimatic Index. The model suggests coastal areas of KwaZulu-Natal, Eastern Cape and Western Cape provinces to be climatically suitable. Climatic suitability is also suggested for parts of Northern provinces such as Mpumalanga, Limpopo and the North West. Central and western provinces such as the Free State and Northern Cape are projected as being unsuitable, primarily due to dry or cold stress.

Future climate

The potential distribution of lantana under future climate scenarios show a substantial contraction in climatically suitable areas in the northern provinces of Limpopo and Mpumalanga as well as coastal areas of Western Cape

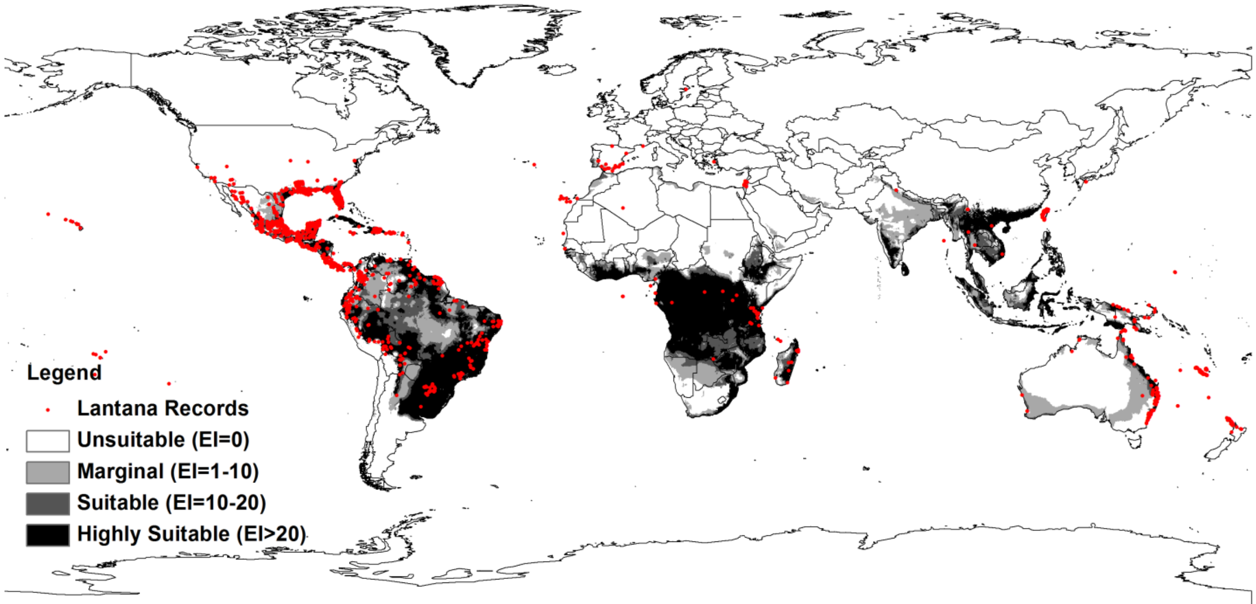

Figure 1. The current global distribution of lantana based on records taken from the Global Biodiversity Information Facility 2007 together with the current potential global distribution of lantana modelled by CLIMEX for reference climate (averaging period 1950-2000).

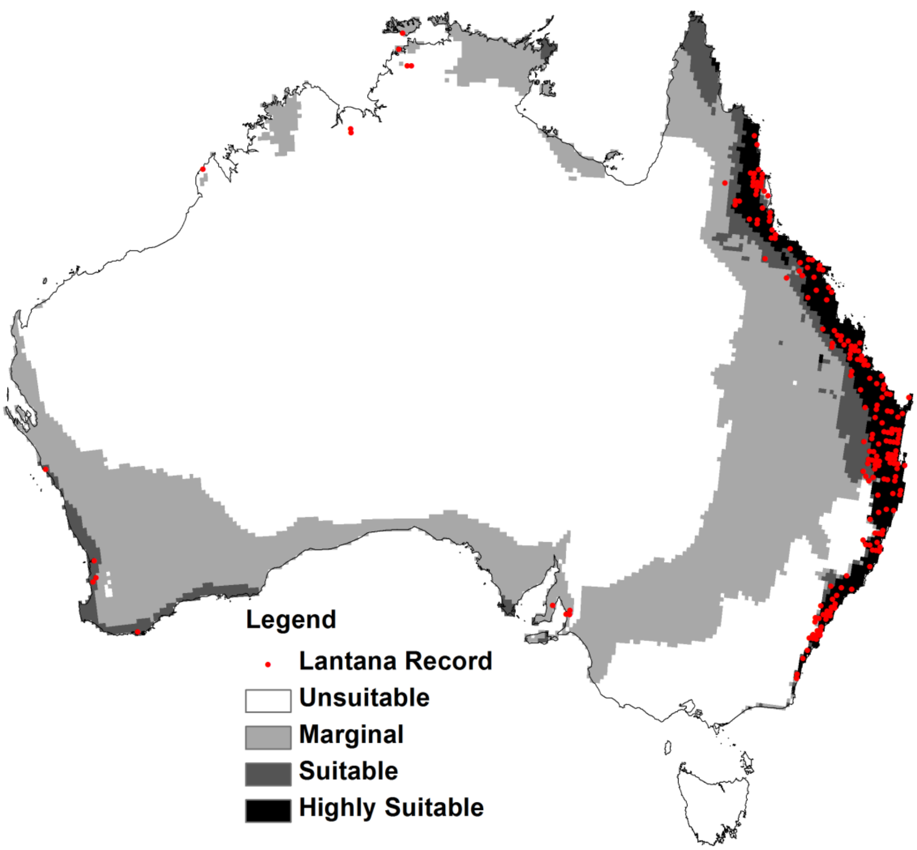

Figure 2. Current Australian distribution of lantana based on records from Australia's Virtual Herbarium together with the current potential distribution of lantana modeled by CLIMEX for reference climate (averaging period 1950-2000).

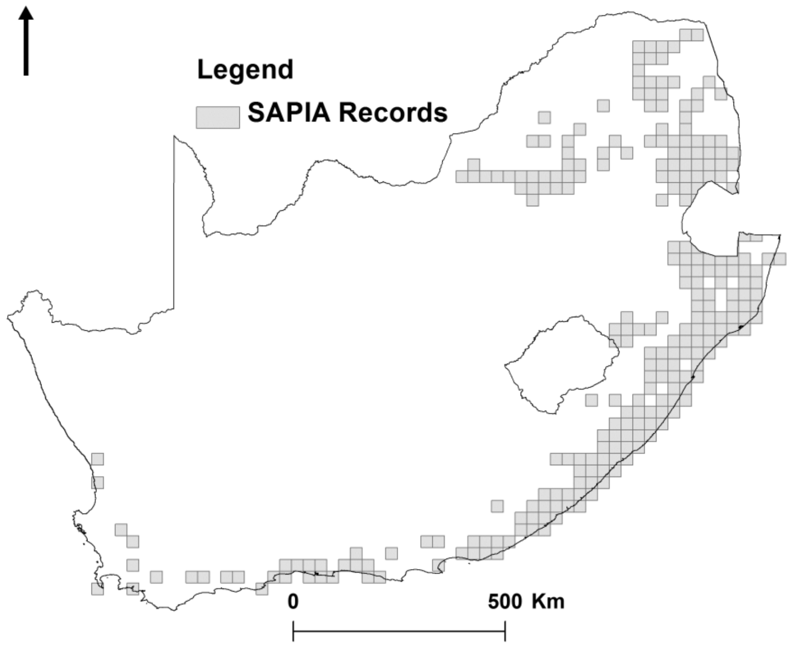

Figure 3. Distribution and relative abundance of lantana in Southern Africa (Southern African Plant Invaders Atlas Database, 2006).

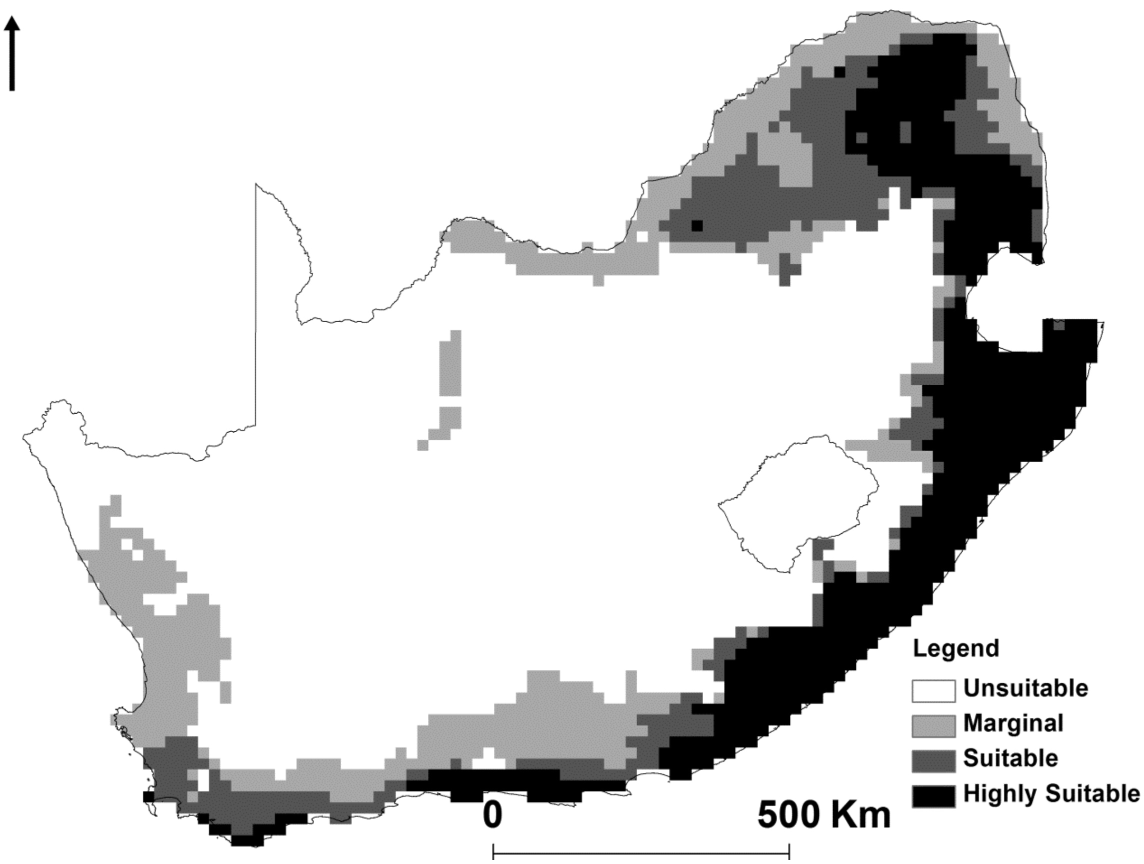

Figure 4. The climate (EI) for lantana in South Africa based on CLIMEX under historical climate (averaging period 1950-2000).

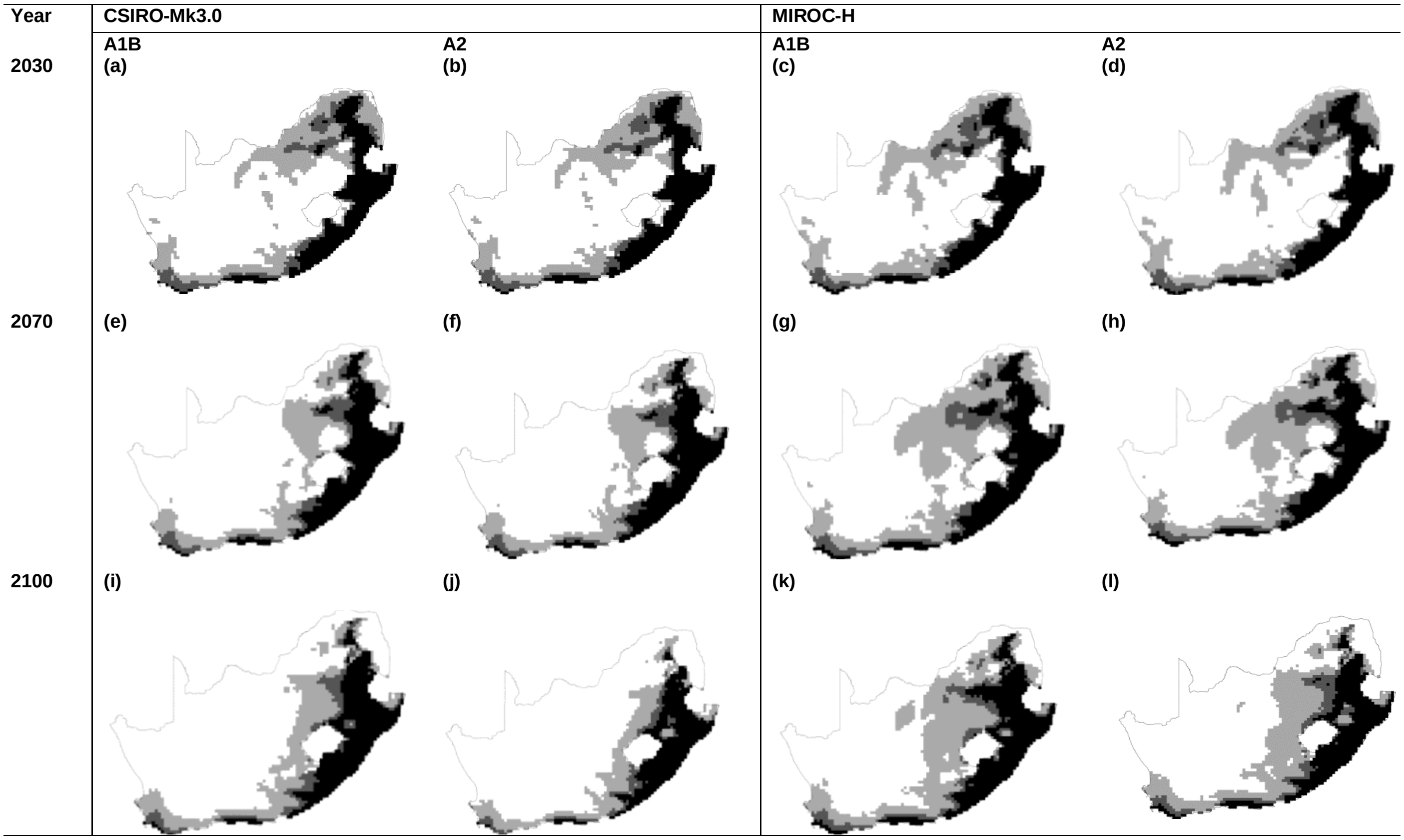

Figure 5. The climate (EI) for lantana in three time periods projected using CLIMEX under the CSIRO-Mk3.0 and MIROC-H GCM running the SRES A1B and A2 scenarios.

province and this trend was exacerbated by 2100 (Figure 5). The contraction in climatically suitable areas was more pronounced in the results shown by the CSIRO-Mk3.0 GCM as compared to the MIROC-H GCM. However, very little variation was seen between the two emission scenarios. The results also show that, in the future, lantana's potential distribution may expand further inland into new areas in KwaZulu-Natal and Eastern Cape provinces. This projection was consistent for both the GCMs.

DISCUSSION

The validation using Australian distribution data showed a good match with the modelled climate suitability for the continent. A good fit was also observed between model output and the current global distribution records as well as the current South African distribution. Under current climate, the model projects coastal areas of KwaZulu-Natal, Eastern Cape and Western Cape provinces and parts of Northern provinces such as Mpumalanga, Limpopo and the North West to be climatically suitable. A previous study (Rouget et al., 2004) that utilized climatic envelope models (CEMs) to assess the potential distribution of invaders (lantana was one of the species that was assessed) in South Africa found that under current climate, some of the worst perceived invaders in the country had less potential to increase in range as compared to other species (Le Maitre et al., 2000, 2004). Lantana was identified as one of such species. Our assessment of potential lantana distribution under current climate agrees with this assessment. Based on a comparison of Figures 3 and 4, lantana appears to have spread to occupy its potential range. However, it could continue to invade new habitats and increase its density within this range. Furthermore, the results of the climate change modelling show the potential for substantial range expansion in KwaZulu-Natal and Eastern Cape provinces, an assessment also shown in a study conducted by Vardien et al. (2012). Therefore, it would be prudent to formulate management strategies that would prevent lantana from expanding its range in the Eastern Cape and northern KwaZulu-Natal. These could include the formation of strategic containment lines or quarantine barriers. Land managers in these regions need to be alerted to the long term threat and undertake on-going monitoring of the identified areas. In such instances, the maps resulting from this study are useful tools for informing individuals and organizations involved in invasive species management. Furthermore, in the short term (2030), provinces such as Limpopo, Mpumalanga and Western Cape remain at risk of invasion consistently under both GCMs although their climatic suitability becomes diminished by 2100. These areas would benefit from a concerted effort of weed control measures in the short term. This would be an effective strategy in terms of reducing impacts on natural resources since climatic suitability is projected to contract for these areas by 2100.

Two factors may affect the accuracy of the results presented here based on the assumptions underlying the modelling process. First, CLIMEX does not explicitly incorporate the effects of non-climatic factors that affect species' distributions such as dispersal potential, biotic interactions, topography, land-use and disturbance activities. The main assumption underlying this modelling environment is that climate is a major determinant of species' distributions although other factors can be considered in a stepwise fashion after the climate modelling has been completed. Second, the results are only indicative of the direction and magnitude of change that may be expected in the future due to the uncertainties associated with the state of climate modelling and uncertainty in future global greenhouse gas emission patterns (Kriticos et al., 2006). The maps show areas of climatic suitability for lantana and are not predicted future distributions. The dispersal capability of lantana and efforts on the part of land managers to curb its proliferation may cause the actual range of the species to fall below the potential.

Lantana has had a profound negative impact on biodiversity, water resources and agriculture in South Africa (Le Maitre et al., 2000, 2004), and, thus, the potential distribution maps presented here can be used to develop broad strategic control plans so that the management of this noxious weed can be adapted to the challenges of climate change. In particular, they can inform decisions concerning the effective allocation of resources for weed management in the short term and also the long term. An additional impact of climate change will be on biocontrol agents that are being used for biological control of lantana since the distribution of such agents will also likely alter with climate change (Kriticos et al., 2009). This is particularly pertinent given the considerable amount of resources that have been used in the biological control of lantana in South Africa. Ongoing monitoring of current lantana biological control programmes will be essential so that changes may be detected early and appropriate action taken. Moreover, disturbance plays a key role in the spread of lantana (Day et al., 2003, Stock et al., 2009), and, therefore, it would be practical to focus management strategies on reducing disturbance. This is particularly true for protected areas such as national parks and nature reserves as these contain environmental assets of high conservation value. For example, roads and rivers may provide channels for disturbance through propagule dispersal or creation of open spaces (Alston and Richardson, 2006). Therefore, eradication of existing infestations around such disturbances together with on-going monitoring to avoid re-infestation should form part of the management strategy to reduce the chances of further spread through protected areas. There will always be a need to control lantana in areas containing biodiversity of high conservation value because of its characteristics as a highly competitive weed. In such cases, the results from this study can inform targeted management actions, particularly where climatic suitability has been projected to increase in conservation areas under climate change. However, a recent study has shown that, despite intensive management of lantana in Australia, India and South Africa, little evidence exists for success. An adaptive management approach has been suggested which focuses on the positive qualities of this species rather than the negative qualities (Bhagwat et al., 2012). The results presented here can also be useful under such a scenario by identifying areas where such innovative management approaches can be tested without further endangering biodiversity.

Conflict of Interests

The author(s) have not declared any conflict of interests.

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