

Accommodating scenarios of climate change and management in modelling the distribution of the invasive tree *Schinus molle* in South Africa

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Determining the potential range of invasive alien species under current conditions is important. However, we also need to consider future distributions under scenarios of climate change and different management interventions when formulating effective long-term intervention strategies. This paper combines niche modelling and fine-scale process-based modelling to define regions at high risk of invasion and simulate likely dynamics at the landscape scale.

Our study species is *Schinus molle* (Peruvian pepper tree; Anacardiaceae), a native of central South America, introduced to South Africa in about 1850 where it was widely planted along roads.

Localities of planted and naturalized trees were mapped along 5380 km of roads – a transect that effectively samples a large part of western South Africa. Correlative modelling was used to produce profiles of present and future environmental conditions characterizing its planted and naturalized ranges. A cellular-automata simulation model was used to estimate the dynamics of *S. molle* under future climates and different management scenarios.

The overall potential range of *S. molle* in the region is predicted to shrink progressively with predicted climate change. Some of the potential range of *S. molle* defined based on current conditions (including areas where it is currently highly invasive) is likely to become less favourable. The species could persist where it is well established long after conditions for recruitment have deteriorated. Some areas where the species is not widely naturalized now (notably the fynbos biome) are likely to become more favourable. Our modelling approach allows for the delineation of areas likely to be invaded in future by considering a range of factors at different scales that mediate the interplay of climatic variables and other drivers that define the dimensions of human intervention such as distance from planted trees and the density of planted plants, both of which affect propagule pressure.

Successful invasion of an introduced plant species depends on many factors, including the climate and physical environment, features of the recipient ecosystem, lifehistory traits of the invader, and the availability and abundance of propagules (Richardson and Pyšek 2006). Management initiatives are underway around the world to tackle problems associated with invasive alien species. These range from local-scale efforts to eradicate particular species to systematic management programs at the scale of landscapes or regions. Limited resources and the increasing extent of invasions make it essential to prioritize species and areas for management (Nel et al. 2004).

For individual invasive species, a major challenge is to determine the potential range of suitable environmental conditions. This influences the importance attached to the species and its priority for management attention at different temporal and spatial scales (Rouget et al. 2004). A problem is that many invasive species have had short residence times and have had inadequate time to sample all potentially invasible habitats. Human factors are important mediators of the geographic ranges of invasive plant species (Thuiller et al. 2006). Sites of introduction in relation to the overall suitable range and propagule pressure are crucial determinants of invasive range (Wilson et al. 2007). Despite the realization of the importance of these factors, they are seldom considered when assessing the distribution limits of invasive species. One reason for this is that records of failed introductions are generally poor. Alien trees planted for

ornamentation and amenity purposes offer good opportunities for gaining insights regarding the role of human activities in shaping distribution range.

Potential distributions can be determined using speciesdistribution models (also called niche models); this involves correlating the presence/absence of a species with environmental conditions to determine its potential range (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Heikkinen et al. 2006). Niche modelling has several inherent constraints, including difficulties in extrapolating current patterns onto new environments over which the models have not been fitted. Also, models are static in space and time and are conceptually unable to deal with nonequilibrium situations, since they do not distinguish between the transient and equilibrium responses of species to a stochastically and dynamically changing environment (Guisan and Thuiller 2005). Consequently, they cannot accommodate migration in a dynamic way. To address this limitation, recent risk-assessment analyses for climatechange scenarios have commonly used two crude assumptions about migration: no migration beyond a species' present site ("zero migration" or "null migration") and perfect migration to all sites, or "full migration" (Peterson et al. 2002, Thuiller 2004). These approximations bracket the most optimistic and pessimistic estimates of future species range size, but have so far incorporated only the simplest migration limitations - i.e. migration into contiguous elements of the modelled landscape (Peterson et al. 2002) – to refine these estimates.

Several recent studies have shown that such modelling can be made more realistic by linking niche models with mechanistic models that consider aspects of demography and dispersal (Roura-Pascual et al. 2009). If concerned about the fine-scale dynamics of a given species, e.g. with reference to potential management interventions, we must know the capacity of the species to disperse and track suitable conditions. To this end, one may utilize a model which simulates the spread of a species based on its ability and mode of dispersal, while using the niche model to determine the general suitability of a region for the species i.e. the likelihood of individuals establishing at different locations within the new region (Engler and Guisan 2009). This approach utilises non-spatial, species-specific attributes and spatially-explicit climatic attributes to predict the potential spread of the target species in time and space. The distribution changes can then be used as inputs to objective management plans for a recently introduced invasive species.

In this paper we examine the distribution of planted versus naturalized individuals of the alien tree *Schinus molle* over large parts of South Africa. Our aims are: 1) to produce accurate profiles of environmental conditions (biophysical and those related to human activities) that characterize the two types of range of this species: planted and naturalized (self-established individuals), by using correlates of distribution via boosted regression trees (BRT); 2) to predict changes in distribution of naturalized plants due to climate change using BRTs based only on climate-related variables; and 3) assess effects of potential management strategies and changes in climate using a simple cellular-automata simulation model. Insights from these investigations are

needed to formulate long-term intervention strategies for this species.

Materials and methods

Species occurrence and environmental data

Schinus molle (Peruvian pepper tree; Anacardiaceae) is a long-lived and drought-tolerant evergreen dioecious tree native to the arid central region of South America. It can flower at any time of the year and female trees bear a mixture unripe and ripe fruits most of the time making their seeds available for dispersal throughout the year (Milton et al. 2007). Seeds are dispersed by birds, mammals, and in running water, and seedlings become established in washes, ravines, old fields, and rock outcrops (Howard and Minnich 1989). Growth is greatest in the warm season until soil moisture is depleted (Nilsen and Muller 1980a, b). With continuous seed production and reliable dispersal the major barrier to establishment seems to be germination and seedling survival. Saplings are hardy and survive nearly everywhere that they planted (Nilsen and Muller 1980, Howard and Minnich 1989). It was introduced to South Africa in about 1850, and since 1950 was widely planted, especially as a shade tree at picnic sites along major roads. In the last two decades it has become highly invasive in semi-arid savannas (Iponga et al. 2008b) and is now listed as a major invader (Nel et al. 2004).

The range of the species was recorded during a survey along 5380 km of roads in regions of South Africa where S. molle is known to be naturalized or invasive and occur at high densities: mainly the Eastern Cape, Free State, Northern Cape and the Western Cape provinces (Fig. 1). The species also occurs in other provinces (Henderson 2001), but at very low densities (unpubl.). We mapped all planted and self-established ("naturalized" sensu Pyšek et al. 2004) individuals along the roads using a GPS. Individuals were mapped as "planted" where their position in the landscape clearly indicated planting by humans - e.g. regular pattern, proximity to picnic sites, roads, human settlements. We also surveyed areas of radius 100 m around each mapped planted and naturalized individual to search for self-sown plants (an initial survey revealed that almost all naturalized plants were captured in surveys moving this distance from planted trees). Planted and naturalized individuals were recorded at 384 localities (2212 individuals) and 317 localities (1575 individuals) respectively (Fig. 1; see also Supplementary material Fig. S1). Does the sampling strategy (exclusively along roads) bias the results of the modelling exercise? We believe not, since the road transects ensured excellent sampling of all major habitats and bioclimatic regions, and was the most cost-effective strategy for thorough sampling.

Occurrence data were then correlated with various environmental data using niche models to assess the suitable range for both planted and naturalized individuals separately. We used climatic, topographic and land use variables that are known to influence the distribution of the plant species in South Africa (Thuiller et al. 2006, Wilson et al. 2007), and variables related to history of the invasion to explain the distribution of naturalized individuals.



Figure 1. Roads surveyed for the presence of planted and naturalized individuals of *Schinus molle* in South Africa. The density of planted and naturalized individuals is shown in Fig. 2. Shading shows major terrestrial biomes (Mucina and Rutherford 2006). The dashed line encloses the study domain. Images show: trees planted along a road (a); self-sown individuals growing in Kimberley's Big Hole (b); and naturalized individuals along a river (c). Photos: D. M. Richardson (a), D. M. Iponga (b) and S. J. Milton (c). For separate maps showing localities of planted and naturalized individuals, see Supplementary material, Fig. S1.

The climatic parameters used were: minimum temperature of the coldest month (*mtc*), growing degree days (*gdd10*), mean annual precipitation (*map*), and mean annual potential evapotranspiration (*pet*). The South African Atlas of Agrohydrology and Climatology climate-surface dataset (Schulze 1997) covering southern Africa at a resolution of 1 minute by 1 minute (~1.6 km at this latitude) was used to represent current climate, along with more recently constructed rainfall surfaces (Lynch 2003). In addition, growing degree days (*gdd10*), a heat sum of average temperatures above 10°C, was derived from the monthly average climate surfaces. Distance to "main rivers" (*driv*; scale 1:500 000; Nel et al. 2007), "human footprint" (*hfoot*;

original resolution 1×1 km; Sanderson et al. 2002), and biomes (*biome*; Mucina and Rutherford 2006) were also used in most analyses (Table 1). Distance to rivers was deemed useful since rivers provide ideal sites for the establishment, growth and dispersal of this species (unpubl.). The human footprint represents the degree of human-mediated modification of environments, through agricultural practices, urbanization and other factors; these factors are known to influence the distribution of *S. molle*. Other variables were also generated to determine the importance of history in naturalization of *S. molle*: distance to the nearest planted individual (*dsp*), and a proxy for propagule pressure (*propres*), computed by dividing pixels at

Table 1. The relative influence of variables in different models used to predict environmental suitability for *Schinus molle* under current conditions and under climate change. Environmental variables: mtc = minimum temperature of the coldest month; gdd10 = growing degree days (annual temperature sum above 10°C); map = mean annual precipitation; pet = annual potential evapotranspiration; driv = distance to main rivers; biome (Table 2); hfoot = human footprint (representing the total ecological footprint of human populations, see text); propres = proxy for propagule pressure (computed using ArcGIS 9.3 (ESRI), by dividing pixels at 1' × 1' (1.6 × 1.6 km) into 100 smaller pixels and counting the number of pixels occupied by planted species (sources of propagules); dsp = distance to the nearest planted individual. Niche models: planted = model based on the distribution of mapped planted individuals; naturalized = model based on the distribution of naturalized distribution including distance to the nearest planted individual; NatPropres = model built with naturalized distribution including a proxy for propagule pressure; NatCc = model built with naturalized distribution including only climate variables.

Model		Variables relative influence (%)								AUC
	mtc	gdd10	тар	pet	driv	biome	hfoot	propres	dsp	
Planted	14.7	4.8	35.6	33.1	1.2	6.7	3.8	_	_	0.91
Naturalized	28.1	6.7	18.3	17.7	15.6	5.2	8.4	_	_	0.94
NatDsp	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0	99.7	1.00
NatPropres	1.5	0.9	6.6	9.3	20.4	8.3	5.6	47.5	_	0.98
NatCc	31.2	12.3	31.4	25.1	-	-	-	-	-	0.93

 $1' \times 1'$ (i.e. 1.6×1.6 km) into 100 smaller pixels and counting the number of GPS localities of planted individuals. All variables were prepared at $1' \times 1'$ grid resolution to match the climatic data set in ArcGIS 9.3 (ESRI); vector variables were directly rasterized at this resolution, while raster variables (i.e. *hfoot*) were upscaled.

Potential distribution: planted vs naturalized individuals

We used boosted regression trees (BRTs; Ridgeway 1999, Friedman 2001, Friedman and Meulman 2003) to elucidate ecological differences between planted and naturalized individuals of *S. molle* across its South African range. BRT uses an iterative method (the boosting algorithm) for developing multiple regression trees and combining them into an ensemble prediction (Friedman and Meulman 2003). Regression trees are built by splitting the calibration data repeatedly, according to a simple rule based on a single explanatory variable. At each split, the data are partitioned into two exclusive groups, each of which is as homogeneous as possible (Breiman et al. 1984). BRTs were used because their predictive performance and reliable identification of relevant variables have been clearly demonstrated (Elith et al. 2008).

We first distinguished between occurrences corresponding to planted individuals (planted) and naturalized individuals (naturalized). Since absence data were not available, we generated random pseudo-absences at localities along the surveyed roads without confirmed presence of the species and at a distance >100 m away from any planted or naturalized individual. This could include a proportion of false absences that do not necessarily represent areas that are environmentally unsuitable. Each occurrence dataset was then divided into training (70%) and testing (30%) sets to calibrate and evaluate model performance, respectively. To reduce uncertainty due to the re-sampling procedure, we calibrated 10 replicate BRT models for each occurrence dataset by randomly creating 10 different sets of both training and testing occurrences. Each set of 10 replicate predictions were averaged at equal proportions to produce a unique ensemble estimate of the area suitable for S. molle. Additionally, BRTs also estimated the relative importance of each environmental variable included into each replicate model by accounting for the rest of the variables (Thuiller et al. 2006). As in the final ensemble predictions, we also computed the averaged influence of each environmental variable to understand their importance in explaining the potential distribution of planted and naturalized populations of S. molle separately.

Since naturalization of *S. molle* is also influenced by other non-environmental factors, we calibrated two extra models to explore the importance of the history of the invasion in explaining the current distribution of the naturalized individuals of the species. The first model was calibrated using all the previously mentioned environmental data as well as the distance to planted species and propagule pressure (NatDsp). The second model used only propagule pressure (NatPropres) (Table 1). The occurrence data used to develop these two last models only included records of naturalized individuals.

Occurrence data not used in model development (30%) was used to calculate the area under the curve (AUC) of the Receiver Operator Characteristic (ROC), which evaluates model performance independently of the arbitrary threshold of the prediction (Thuiller et al. 2006). Following the scale of Swets (1988), prediction was considered random when it did not differ from 0.5, poor when it was in the range 0.5-0.7, and useful when in the range 0.7-0.9. Predictive accuracy > 0.9 was considered good to excellent (1 = perfect). AUC values under 0.5 reflect counter predictions (omission and commission rates higher than correct prediction). Because of the incomplete sampling in eastern and north-eastern parts of the country, we restricted our predictions to western South Africa (Fig. 1) to avoid projecting the model into areas outside the range of calibration (Randin et al. 2006). We confirmed that the range of environmental conditions covered by the road sampling was also representative of the rest of the region by comparing the range of the environmental variables present in the sampled roads with the range present at the overall region.

Potential distribution of naturalized individuals of *Schinus molle* under climate change

To estimate changes in the potential distribution of S. molle with climate change (step 2), we determined a niche model based on only naturalized occurrence data and using a smaller set of climatic variables for which data are available for both present and future conditions (NatCc) (Table 1). As described previously, we developed 10 replicate models and projected them onto present-day conditions (to test the performance of the models) and two scenarios of future climate. Future climate predictions were produced by perturbing the current climatic data with anomalies derived from climatic simulations produced by the HADCM3 General Circulation Model (GCM) (Gordon et al. 2000) using the A2 and B2 IPCC SRES scenarios (Nakicenovic and Swart 2000), downloaded from the IPCC-DDC, in accordance with guidelines for climate impact assessment (IPCC-TGCIA 1999, IPCC-TGICA 2007) using a technique described by Hewitson (2003). Absolute anomalies were used for the temperature variables while relative anomalies were used for the rest. Potential evapotranspiration (pet) surfaces were calculated using the FAO 56 Penman Monteith combination equation (Allen et al. 1998). Hewitson (2003) considers this technique of perturbing detailed current climate surfaces with coarser GCM anomaly surfaces appropriate for a range of scales, capturing the spatial differences of the existing climate while maintaining the large-scale response of the GCM. We chose HADCM3 because it represents a fairly extreme projection of future climate for the southern African region (Rousteenoja et al. 2003).

Spread of *Schinus molle* under different management strategies

Few studies have connected species spread with niche models for prediction of range expansion for a species with known level or density of invasion (Inglis et al. 2006).

We used a very simple model based on the principle that the species will spread faster in areas that are most suitable for the growth of the species. The previous climate-change predictions for both present and future (A2 and B2) climates were then incorporated into the simulation model to predict changes in distribution of naturalized individuals of S. molle under different management scenarios over the next 100 yr. As suitability maps for the climate-change scenario were only available for 2000, 2050 and 2100, the suitability maps for the intermediate years (in ten year steps) were linearly interpolated. We used a cellular automata model with these simple rules: 1) the cell size was $1' \times 1'$ (i.e. 1.6×1.6 km); 2) one time-step represents 10 yr (time needed for one individual to reach maturity; Iponga et al. 2008b), and we assumed that all plants were mature at the beginning of a time-step; 3) each individual produced a maximum of 50 surviving offspring in one time-step, based on seed production and seedling survival of this species (Iponga et al. 2008a, 2009a). This reproduction was dependent on the suitability of the cell, with no reproduction taking place when suitability values were below 0.42 (based on the model built with naturalized distribution including only climate variables, NatCc), and production of 50 offspring with a suitability of 1.0, with linear interpolation for intermediate value; These suitability thresholds were determined by analyzing the suitability values for the localities with naturalized individuals: 95% of them were found in areas with suitability levels between 0.42 and 1; 4) we assumed arbitrarily that 10% of the offspring were dispersing and establishing in the eight neighbouring cells. The remaining 90% established in the original cell; 5) we distributed the dispersers equally into all eight neighbouring cells, independent of their occupancy status. All dispersers arriving in a cell were then summed. Each cell could hold a maximum of 341 874 individual plants.

The different management scenarios tested were: a "business-as-usual" scenario (NM) (i.e. no further plantings, no control operations); doubling the number of planted individuals along surveyed roads (P) (i.e. further planting for shade and amenity use); removing only planted individuals along the surveyed roads (C) (i.e. a pro-active management strategy aimed at removing sources of propagules); and removing all planted and all naturalized individuals in a cell $(1' \times 1')$ from the planted one (CC). To determine the number of cells and the number of trees planted per cell under scenario P, we selected at random empty cells along the sampled roads and "planted" a randomly drawn number of trees following a Poisson distribution with lambda = 6 (as determined by plotting the frequency distribution of planted individuals found in the field) until the number of planted individuals was doubled.

To obtain a general pattern of occupancy of *S. molle* under different management scenarios, we calculated the change in occupied cells between NM (no management) and other management scenarios under the three climate-change scenarios (A2, B2, and no change) for 2050 and 2100. For each cell, we subtracted the occupancy value (1: occupied, 0: not occupied) of the NM scenario from the occupancy value of one of the other three management scenarios and added the differences (-1: cell not occupied with management but occupied without management; 0: no

change; 1: cell occupied with management but not occupied without management) from all cells in the simulated area. This resulted in one value per year per scenario which characterizes the net change of occupancy in the simulated area. A positive value indicates more cells occupied than in the NM scenario, a negative number indicates less. We also selected three regions, centred on Towerberg (Nama-karoo biome), Touwsriver (succulent karoo biome) and Kimberley (savanna biome), to illustrate differences at fine spatial scales after running the spread models. These regions were selected because they fell along a rainfall gradient (winter rainfall; all-year rainfall; summer rainfall) and because all had high numbers of *S. molle* individuals at present.

Results

Potential distribution of *Schinus molle*: planted vs naturalized individuals

Models were successful in generating both planted and naturalized present-day known distributions of S. molle in western South Africa, with AUC values of 0.91 (planted) and 0.94 (naturalized) (Table 1). These models were calibrated incorporating climatic and topographical variables. For planted, the most influential variables for predicting S. molle environmental suitability were: mean annual precipitation (map), annual potential evapotranspiration (*pet*) and minimum temperature of the coldest month (*mtc*). For naturalized the most important variables were: minimum temperature of the coldest month (mtc), mean annual precipitation (map), annual potential evapotranspiration (pet), and distance to rivers (driv) (Table 1). Despite reasonable propagule pressure (Table 2 and Fig. 2b), only a small part of the fynbos biome is suitable for establishment of this species under current conditions (Fig. 3). When propagule pressure (propres) and distance from naturalized individuals to planted trees (dsp) were added to the model estimating the distribution of naturalized individuals (NatDsp and NatPropres), dsp emerged as the most important and sole variable explaining the presentday distribution of S. molle. Propres also emerged as important when *dsp* was omitted (Table 1).

Not surprisingly, the model planted yielded a larger potential range of suitable conditions than naturalized (Fig. 2a, b, respectively). The models revealed that the largest area of suitable habitat for the establishment of *S. molle* without human assistance occurs in the Nama- and succulent-karoo biomes, followed by savanna, grassland, and Albany thicket biomes (Fig. 3).

Potential distribution of naturalized individuals of *Schinus molle* under climate change

Our aim was to assess the potential of the species to occupy natural areas in the future. Consequently, our predictions were obtained from a model calibrated using only naturalized occurrences and climatic data (layers of potential changes in human-activity factors were not included; see Materials and methods). This model performed well in predicting present-day occurrences (AUC = 0.93) (Table 1, NatCc), and showed little difference in terms of suitable

Table 2. Number of cells $(1.6 \times 1.6 \text{ km})$ in each biome sampled during the field survey (Sampled), containing planted individuals (Plant) and containing naturalised individuals (Nat). Percent indicate the percentage of cells in relation to each biome's size (Size, presented as number of cells). The invasion ratio is calculated as the number of cells with naturalized plants (Nat) divided by the number of cells with planted individuals of *Schinus molle* (Plant).

Biomes	Size		No. of cells		Percent			
		Sampled	Plant	Nat	Sampled	Plant	Nat	
All	421877	3083	244	132	0.73%	0.06%	0.03%	0.54
Savanna	136014	330	20	15	0.24%	0.01%	0.01%	0.75
Grassland	119810	393	13	14	0.33%	0.01%	0.01%	1.08
Nama-Karoo	88185	979	114	62	1.11%	0.13%	0.07%	0.54
Coastal Belt	5249	0	0	0	0.00%	0.00%	0.00%	NA
Desert	2404	12	0	0	0.50%	0.00%	0.00%	NA
Succulent karoo	29657	293	30	18	0.99%	0.10%	0.06%	0.60
Fynbos	29588	841	39	9	2.84%	0.13%	0.03%	0.23
Álbany thicket	10970	235	28	14	2.14%	0.26%	0.13%	0.50

areas compared to the model using a broad set of environmental layers (Fig. 4 compared to Fig. 2, panel N2). As in this naturalized model, the most relevant variables for predicting the climate suitability of *S. molle* were: minimum temperature of the coldest month (*mtc*), mean annual precipitation (*map*), and annual potential evapotranspiration (*pet*) (Table 1, NatCc).

When projecting this model onto future scenarios A2 and B2, the potential range of *S. molle* was generally predicted to shrink progressively under both scenarios of climate change. The area predicted as suitable for the species now (32.4%) is expected to shrink considerably: 16.7% suitable area under scenario A2 and 23.5% suitable area under scenario B2 in 2050; and 6.4% and 8.4% under scenarios A2 and B2 respectively in 2100 (Fig. 4). This reduction in area suitable for *S. molle* is expected to affect all biomes, but to be less pronounced in the grassland and fynbos biomes (Fig. 5, blue lines).

Spread of *Schinus molle* under different management strategies

According to the spread model, about 10% of Albany thicket and Nama-karoo respectively will be invaded under both A2 and B2 climate change scenarios by 2100 (Fig. 5, red line). Less area (<5% of the total area of the respective biome) is predicted for the fynbos and succulent karoo biomes, while savanna and grassland biomes showed very low potential spread (Fig. 5, red line).

Differences in the total number of occupied cells with no management and under the three scenarios of active management suggest that *S. molle* will increase its distribution (more cells occupied) under all planting scenarios (Table 3). Not surprisingly, highest cell occupancy occurred under management scenario P for all climate-change scenarios for both 2050 and 2100, while scenario CC generated the lowest cell occupancy (Table 3).

Different patterns were observed at local scales in the three selected study areas (Fig. 6). The number of occupied cells in the Kimberley area increases exponentially during the first 30 years under all management and climate scenarios, but then shows little increase of spread under both A2 and B2 climate-change scenarios. The other two areas show an increase in cell occupancy over time under all scenarios. However, while the rate of spread in Touwsriver is maintained over time, that for Towerberg shows a slight deceleration (Fig. 6). In any case, all areas show the highest levels of occupancy under management scenario NM and P (Fig. 6).

Discussion

We first mapped two categories of distribution (planted and naturalized) of an alien species *S. molle* in South Africa, then determined the bioclimatic features of the two distributions in the major terrestrial biomes and finally assessed the climate suitability of the species under different climate changes scenarios. Additionally, we combined this information on future climatic suitability with various management scenarios using a simulation spread model to identify areas that may be most susceptible to invasion by *S. molle* in South Africa.

Potential distribution of *Schinus molle*: planted vs naturalized individuals

A large part of western South Africa is potentially suitable for growth and naturalization of S. molle. The area identified as suitable for growth of planted individuals is larger than the area identified as suitable for naturalization of the species. Differences in the two predicted ranges (Fig. 2c) are instructive. Areas suitable for growth of planted individuals but not naturalization represent areas where environmental conditions are currently unfavourable for establishment. Several studies have tested the value of niche modelling for assessing the risk of plant species from other region invading a given area (Curnutt 2000, Richardson and Thuiller 2007). The potential species distribution is projected on the assumption that current niches reflect species environmental preferences, which is retained in the invaded new areas (Beerling et al. 1995). The larger suitable area for planted than naturalized plants (Fig. 2a vs b) is attributable to the role of nurturing by humans of planted trees (e.g. by watering, nutrient supplementation, and removal of competing vegetation) which improves growth and survival (Iponga et al. 2008b). Areas shaded in red in Fig. 2c are zones where (presumably largely abiotic) barriers preclude invasion by thwarting recruitment. Previous studies have shown that predicted potential distribution is



Figure 2. Predicted environmental suitability for *Schinus molle* modelled using locations of planted and naturalized individuals via boosted regression trees (see text). Maps show the current predicted suitability for planted (a) and naturalized (b) individuals in each cell, and in panel (c) areas suitable only for planted (red), only for naturalized individuals (blue), and areas suitable for both (black).

generally more extensive than actual distribution (Peterson et al. 2002, Pearson and Dawson 2003). The main focus of this study is on areas that are susceptible to invasion by *S. molle* – areas shaded in blue and black in Fig. 2c under prevailing climatic and management conditions. The delineation of these areas is influenced by the interplay of climatic variables with other factors that define the dimensions of human intervention such as distance from planted trees and the density of planted plants, both of which affect propagule pressure (Rouget and Richardson 2003, Foxcroft et al. 2004). However, 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 (Huntley et al. 1989, Beerling et al. 1995).

At the biome level, our models show that the Nama- and succulent karoo biomes are clearly most affected by S. molle naturalization. Although S. molle has also been planted in the fynbos biome, naturalization in this biome is sparse (Fig. 2b). Preliminary modelling by Rouget et al. (2004) also showed that arid areas were most vulnerable for further invasion of this species. However, not all arid areas that were sampled face naturalization and invasion by S. molle; localised areas, mostly in the succulent- and Nama-Karoo biomes, are affected. These results are supported by studies demonstrating evolutionary conservation of ecological niches and phylogenetic inertia of species across time scales (Huntley et al. 1989, Beerling et al. 1995), because S. molle occurs in similarly arid areas in its native ranges (Howard and Minnich 1989, Goldstein and Coleman 2004). Mean annual temperature of the coldest month (mtc), mean annual precipitation (map) potential evapotranspiration (pet) and proximity to rivers (driv) are most important variables explaining the naturalized distribution of S. molle in western South Africa. Proximity to rivers together with propagule pressure explained local patterns. In the more arid areas, S. molle invades mostly along perennial and ephemeral rivers. River beds probably act as conduits for seed dispersal via frugivorous birds and water and provide microsites for seedling recruitment. Although establishment and spread of alien plants are sometimes limited by an imperfect climate match (Pyšek et al. 2003), local-scale invasions of this species could continue with or without climate change as long as riparian zones provide microsites for recruitment.

Schinus molle can spread in natural habitats without human intervention and can infiltrate naturally-occurring dispersal networks (Milton et al. 2007, Iponga et al. 2008b). All indications are that this species is still at an early stage of invasion, and not at equilibrium with environmental conditions. Consequently, models calibrated using this limited set of occurrence data probably underestimate the potential naturalized distribution of S. molle in western South Africa and represent conservative predictions of the real potential distribution of the species (although the natural experiment of planting along roads has exposed the species to a very broad cross-section of potential sites that exist in the region). The species is expected to expand its range when established individuals mature and act as new seed sources. This caveat must be kept in mind, when reading this paper. Our broad-scale prediction of the potential range of S. molle provides a first approximation for this invasive species that otherwise would be unknown to us.

Potential distribution of naturalized individuals of *Schinus molle* under climate change

It is widely thought that climate change will exacerbate problems with invasive species (Dukes and Mooney 1999), but the many ways in which changes could affect the ranges of species, and the many complex interactions that could



Figure 3. The proportion of the total area of South Africa occupied by each biome, and the area predicted to be suitable for planted and naturalized individuals of *Schinus molle*. Biomes: SV = savanna; GL = grassland; NK = Nama-Karoo; CB = Indian Ocean Coastal Belt; DT = desert; SK = succulent karoo; FB = fynbos; AT = Albany thicket (the distribution of biomes is shown in Fig. 1). Cell classified as "suitable" if the suitability value is larger than a threshold suitability value (the value above which 95% of individuals occur). Thresholds for planted and naturalized trees are 0.2911517 and 0.4058979, respectively.

potentially facilitate or hinder shifts, make accurate predictions very difficult (Thuiller et al. 2007). Also, the ways in which climatic variables will interact in the future may well be different from the current situation. Our models suggest that under both climate-change scenarios examined the area suitable for *S. molle* naturalization is predicted to shrink substantially in the Nama-karoo, succulent karoo and Albany thicket biomes. Climate change will not only alter the suitability for individual species, but is likely to reshuffle species composition and possibly change ecosystem functioning. Such changes are certain to influence environmental suitability and invasibility in ways other than simply through altered climatic tolerance. Nonetheless, it is unlikely that such changes will counter the overall deterioration of opportunities for recruitment and spread over the next century. However, projections of potential future distributions also need to be interpreted with caution. Our approach is based on the assumption that climate is the major driving factor of species distribution (Franklin 1998), and that analysis of the climatic preferences of species can therefore be used to predict areas where the species could occur at regional, continental and global scales. Although climate sets the broad limit of plant species ranges, other factors such as geology, soils, topography, hydrology, disturbance regime, competition and other biotic interactions determine the presence or absence of a species in a



Figure 4. Predicted climatic suitability (for naturalization) of *Schinus molle* in South Africa under two scenarios of climate change (A2 and B2) for the years 2050 and 2100. Predictions were generated using only climatic variables as inputs (see Methods). The panel at top left shows the current distribution of *S. molle* used to calibrate the model, and the surveyed roads without confirmed presence of the species. The panel at top right shows modelled climatic suitability using current climatic conditions.



Figure 5. The percentage of cells per biome suitable for *Schinus molle* (suitability >0.42) (blue lines) and invaded as predicted by the spread model (red lines) in different biomes. Solid lines indicate no climate change (N); dotted and dashed lines show climate-change scenarios A2 and B2, respectively.

particular area and at finer (regional or local) scales (Willis and Whittaker 2002).

Other limitations of this study include uncertainties inherent in climate-change scenarios, the use of coarse resolution GCM anomalies, and the fairly simplistic assumptions about the interactions of input data (Thuiller 2004, Pearson et al. 2006). The relatively coarse scale may also mask potential refuges for species and environmental heterogeneity under climate-change scenarios, especially in areas where the sampling effort was low, leading to potential underestimation of range of conditions that are suitable for the species. The pixel resolution of environmental data may also cloud some finer-scale variations in the species ecological requirements that are not detectable at the spatial scale of our analysis. Because the influence of each environmental variable in determining the species niche is

Table 3. Predicted change in the number of cells occupied by *Schinus molle* under different climate-change and management scenarios for the years 2050 (A) and 2100 (B). Changes were computed as the difference in the number of cells under no management (NM) and other management scenarios (P, C, CC) by subtracting the occupancy layers (value 1 = occupied; 0 = not occupied) of NM scenario from the occupancy layers of the other three management scenarios and summing up all resulting values. Positive values indicate increased occupation with management; negative numbers indicate reduced occupation. Percentages are given in brackets. Climate-change scenarios: N (no climate-change); A2 (temperature rise by 2.8° C in 2080); and B2 (temperature rise by 2.1° C in 2080). Management scenarios: P (doubling the number of planted individuals along surveyed roads); C (removing only planted individuals along the surveyed roads); and CC (removing all individuals from cells in which there are planted individuals).

Climate-change scenario	Management scenarios						
	NM	Р	С	CC			
N	6414	+934 (+14.56%)	-35 (-0.54%)	-71 (-1.10%)			
A2	4256	+806 (+18.93%)	-28 (-0.65%)	-58 (-1.36%)			
B2	5326	+1042 (+19.56%)	-35 (-0.65%)	-72 (-1.35%)			

B) Year: 2100

Climate-change scenarios	Management scenarios						
	NM	Р	С	CC			
N	14365	+1265 (+8.80%)	-22 (-0.15%)	-37 (-0.25%)			
A2	6860	+1288 (+18.77%)	-33 (-0.48%)	-90 (-1.31%)			
B2	9471	+1603 (+16.92%)	-39 (-0.41%)	-85 (-0.89%)			



Figure 6. Spread of Schinus molle under different climate change and management scenarios in three areas of South Africa, each 100 × 100 km in size: Towerberg (coordinates of centre point: 24.53°E, 30.83°S), Touwsriver (20.28°E, 33.30°S), and Kimberley (24.76°E, 28.96°S). The x-axis represents time (from 2000 to 2100, in intervals of 10 yr), the y-axis the number of cells occupied by the species. Three climate-change scenarios are shown in the three rows (N = no change, A2 and B2. In each graph, the four management scenarios are represented by different colours: NM = no management (black) (almost identical with C, therefore not visible in the graphs); P =doubling the number of planted individuals at random along the roads (red); C = removing all planted individuals (green); CC =removing all planted and naturalized individuals in cells which have at least one planted individual (blue).

scale dependent, different degrees of ecological niche variation can arise among populations, depending on spatial resolution of analysis (Wiens 1989). There are also uncertainties related to lags associated with biotic processes. Extensive habitat fragmentation, effects of rising CO₂ concentrations, changing soil conditions and fire regimes, and altered biotic interactions mean that any predictions at this scale must be viewed with some caution. Nonetheless, our results suggest that regions such as Kimberley (currently a "hotspot" of S. molle invasions in South Africa) might be affected relatively early by climate change, but that the region will become less suitable for naturalization over time. This provides managers with a conundrum; S. molle invasions in this region are currently regarded as a serious conservation threat requiring urgent action (Milton et al. 2007, Iponga et al. 2008b). But, is such action justified if the threat is likely to diminish over the next century?

Spread of Schinus molle under different management strategies

To determine the pattern of spread of S. molle in South Africa over the next 100 yr we combined information from climatic suitability under scenarios of climate change and management by means of a simulation spread model. Results indicates that Nama-Karoo and Albany thicket and to a lesser extent succulent karoo and fynbos biomes may experience an increase of S. molle spread under present

and future climatic conditions, even if there was a consistent decline of potential suitability in both future climate-change scenarios beyond 2050 for those biomes. This suggests that although the conditions may not be favourable beyond 2050, the species may have time to expand substantially during the next few decades, and that this may facilitate the spread observed in some biomes. For example, the areas around the town of Towerberg (in the Nama-Karoo biome) and Touwsriver (succulent karoo biome) are predicted to become more susceptible to invasion by S. molle compared to Kimberley (in the savanna biome). This latter area may exhibit a combination of climatic conditions that do not exist within the invasive range, making extrapolation of suitability questionable (Hartley et al. 2006). However, Towerberg and Touwsriver, showing a more constant increase under all climate-change scenarios, may emphasise the risk of invasion faced by the Nama-Karoo and succulent karoo biomes.

The obvious management implication of this finding is that early detection and eradication of this species is important in those areas identified as being highly suitable for naturalization. Schinus molle could persist outside its potential future ranges in the near to medium term because the species is relatively long lived (>100 yr) and produces large quantities of seed. Since the species does not maintain a persistent seed bank (Iponga et al. 2009b), lags in population response of S. molle to deteriorating climatic conditions would be caused by the longevity and droughthardiness of established trees, whereas lags in population responses to improved climatic conditions would be driven by local propagule pressure, plant maturaltion rate and the proximity of potential mates. *Schinus molle* may also be more flexible with regard to its climatic constraints than has been assumed in the spread model, and could persist outside areas predicted to be suitable. The present study confirms the importance of climatic factors in explaining regional patterns of distribution in accordance with other studies at similar scales (Prentice et al. 1992, Franklin 1998).

Problems arising from invasive plants that have value, e.g. as amenity or ornamental species, often leads to conflicts of interest between horticulturists, land owners, municipalities and conservationists (Foxcroft et al. 2008). Schinus molle is still widely used in South Africa as shade tree, especially along roads. Invasion potential could definitely be reduced by promoting the use of local indigenous species as alternatives to alien species, thus reducing further plantings and propagule pressure. Removal of planted and naturalized individuals should start in the areas shown in this study as being at the highest risk of invasion with or without climate change and in areas with large propagule sources. High propagule loads generated by the current invasive populations (e.g. in the Kimberely area) may allow the species to persist and even invade further, even under less ideal environmental conditions. Habitats that function as corridors or have high conservation value, as well as rivers and wetlands in arid areas, should be priorities for clearing within areas currently invaded or at high risk of future invasion as predicted by models calibrated under various climate change scenarios.

Conclusions

We have shown that combining niche modelling (which allows us to define regions at high risk of invasions) and a fine-scale process-based model (to simulate the spread of the invasions at the landscape scale) can yield predictions that are useful for management. Here we discuss some key findings that should inform management strategies for S. molle in South Africa. Firstly, removal of only some plants (e.g. large planted trees along roads) will have little influence because the naturalized plants will soon become seed sources. Clearing of S. molle needs to be prioritized in those areas where environmental suitability is predicted to increase under climate change (Fig. 4). In areas where decreased environmental suitability is predicted, management could be limited to sensitive sites and areas where invasive stands are already having severe impacts on ecosystems (see Iponga et al. 2008b for discussion). Schinus molle has been widely considered a relatively "safe" alien tree until recently. However, its ability to disrupt natural ecosystems has been clearly documented (Iponga et al. 2008b). Despite the evidence provided in this paper which suggests that much of its current range in western South Africa will become less favourable for the species under climate change, the species is already well established over large areas. It may persist long after conditions for establishment have deteriorated. Also, several areas where the species is currently not widely naturalized (notably fynbos and grassland areas) are predicted to become more favourable. Consequently, we recommend that the species should be declared a category-1 invasive species in parts of that country, notably the Eastern Cape, Northern Cape and Western Cape. Category-1 invasive species, according to the Conservation of Agriculture Resources Act, are prohibited on any land except in areas demarcated as reserves for biological control agents; <www.nda.agric.za/docs/act43/ Eng.htm>. The threats posed by the species, effective methods for removing stands and individuals, and good alternatives (ideally native species) need to be publicized.

The approach presented in this study provides a good platform for predicting invasion potential that can be identified and assessed before an invasion takes place and has been used and implemented in invasive species monitoring schemes for emerging invasive species at national and state level in many other countries (Zalba et al. 2000, Welk et al. 2002). The application of the method to S. molle in South Africa has shown its utility, but has also identified key areas of uncertainty that must be considered when interpreting the results. More realistic models of the impacts of climate change on S. molle environmental suitability and range shifts are needed to address the complex interactions between many factors affecting S. molle distribution other than climate, including biotic interactions, evolutionary change and dispersal capacity. The issues highlighted in this paper will guide such work.

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