The potential range of *Ailanthus altissima* (tree of heaven) in South Africa: the roles of climate, land use and disturbance

Running header: *Ailanthus altissima* – an urban invader

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Abstract

Invasive trees are a major problem in South Africa. Many species are well established whereas others are still in the early stages of invasion. The management of invasive species is most cost effective at the early stages of invasion; it is essential to target and contain naturalizing invaders before they spread across the landscape. Multi-scale species distribution models (SDMs) provide useful insights to managers; they combine species-occurrence observations with climatic variables to predict potential distributions of alien species. Applying SDMs in human-dominated ecosystems is complicated because many factors associated with human actions interact in complex ways with climatic and edaphic factors to determine the potential suitability of sites for species. The aim of this study was to determine the degree to which worldwide invader *Ailanthus altissima* has occupied its potential range in South Africa, to identify areas at risk of future invasion. To do this we built a set of SDMs at both global and country scales using climatic, land use and human-footprint data. Climatic data best explained the distribution of *A. altissima* at the global scale whereas variables reflecting human-mediated disturbances were most influential at the national scale. Our analyses show the importance of human-mediated disturbances at a global scale and human occupancy at a country

scale in determining the range limits of *A. altissima*. Populations of this tree species are already present in most parts of South Africa that are environmentally suitable for the species, and management actions need to focus on preventing increases in density in these areas.

Keywords

Biological invasions • Ensemble models • Invasive species • Early stages of invasion • Range filling • Species distribution models • Spread potential • Tree invasions • Urban invasions

Introduction

South Africa has a major problem with invasive alien plant species (Richardson et al. 1997; Henderson 2007). Many species are well established and many others are still in the early stages of invasion (Nel et al. 2004; Mgidi et al. 2007; Wilson et al. 2013). Woody plant species are very well represented in the invasive flora, and species of *Acacia*, *Hakea*, *Eucalyptus*, *Pinus* and *Prosopis* are the dominant invasive plant species in many parts of the country (Richardson et al. 1997). Many other species of alien trees are either recent introductions or have not enjoyed widespread dissemination. Some of these species are well-known invaders in other parts of the world, or have attributes associated with invasiveness, but have not yet expressed their invasive tendencies in South Africa. Some have not yet become naturalized, while others only recently entered the phase of rapid population growth and spread (Nel et al. 2004; Donaldson et al. 2014); a large invasion debt thus exists (Rouget et al. 2015).

Control of invasive alien species (IAS) is most effective at the early stages of invasion (Wittenberg and Cock 2005; Wilson et al. 2016). Early detection and management mitigates widespread impacts associated with the future spread of certain IAS (Wilson et al. 2013, 2016). Species distribution models (SDMs) have been widely applied to determine the potential range of invasive species (Hui and Richardson 2017). SDMs are numerical tools that combine species occurrence observations with environmental estimates to predict distributions across a variety of landscapes (Elith and Leathwick 2009). Management programmes have become increasingly reliant on SDMs to establish the suitability of given areas for particular invasive species and their potential to spread within these areas (Thuiller et al. 2005; Elith and Leathwick 2009; Richardson et al. 2010; Cabra-Rivas et al. 2016).

The suitability of SDMs for modelling the potential ranges of invasive species is however debatable (Guisan and Thuiller 2005; Gallien et al. 2010, 2012; Gassó et al. 2012; Cabra-Rivas et al. 2016). This is because SDMs that are used to model the potential ranges of IAS assume that the environmental conditions in the species' native range are the same as those in its adventive range (Gallien et al. 2012) and that the species being modelled is at quasi-equilibrium with the environment in which it

occurs (i.e. the species is established at all suitable sites and is absent from all unsuitable sites) (Guisan and Thuiller 2005). For this reason, it has been suggested that all available global data from both the native and invasive ranges of the invasive species should be used in determining the "ecological niche" of introduced species (Beaumont et al. 2009; Ibáñez et al. 2009; Gallien et al. 2012). The ecological niche refers to relationships between an invasive organism and its physical and biological environment, which accounts for the effects of both time and space (Shea and Chesson 2002). Such an approach does, however, not account for particular conditions that characterize local ranges (e.g. environment, interactions and human uses) (Gallien et al. 2012). Multi-scale modelling that incorporates a variety of distribution drivers over both the native and adventive ranges is known to improve the overall accuracy of potential species distributions (Sutherst and Bourne 2009; Jiménez-Valverde et al. 2011; Václavík and Meentemeyer 2012). With this in mind, Cabra-Rivas et al. (2016) integrated SDMs from multiple scales to establish the relative importance of various drivers in shaping the distribution of two invasive tree species. They found that climatic variables were the main contributors to the global and country-scale models for both species, followed by land use. The prevalence of climatic over land-use factors in explaining distribution could be because of the climatic heterogeneity within the studied region - the opposite situation could exist in a climatically homogenous region (Cabra-Rivas et al. 2016). At a finer scale, however, human-mediated disturbances were more influential than either climate or land use, a finding supported by a number of other authors (e.g., Rouget and Richardson 2003; Lambdon et al. 2008).

This paper focuses on the tree of heaven (*Ailanthus altissima*), a widespread invasive species in the northern hemisphere (Rejmánek and Richardson 2013) that, for unknown reasons, has yet to become a widespread invader in South Africa. This species is unusual among widespread invasive tree species (see Richardson and Rejmánek 2011 for a global review) in that it is largely an invader of urban habitats (Kowarik and Säumel 2007). This means that climate data of the type typically used to model the range limits of species in SDMs is probably of limited value, since environmental conditions in urban habitats are influenced in complex ways by diverse human activities. The use of human-influenced environmental factors (such as the human footprint indicator) is likely to be more useful for predicting the potential distribution of an urban invader than typical environmental factors (such as broad-scale climatic variables) and it is important to incorporate these into the design of SDMs (Guisan and Thuiller 2005). We aim to evaluate the degree of range filling exhibited by this species in South Africa and to identify areas at risk of future invasion. In a previous study, the current and potential distribution of *A. altissima* was evaluated at a global and country-level for South Africa using a simple bioclimatic envelope model generated in MaxEnt (Walker et al., 2017). Such bioclimatic models usually provide useful approximation of the potential range of species

(Pearson and Dawson 2003; Guisan and Thuiller 2005), but many other factors also influence the distribution of invasive species (Guisan and Thuiller 2005; Cabra-Rivas et al. 2016). Understanding the role of such additional factors is important to inform management strategies. This is particularly important when modelling the spread of invasive species that are not only influenced by natural factors (such as climatic variables) that determine their range limits very broadly, but are also affected by anthropogenic or non-natural factors (such as human-mediated disturbances). Accurately establishing the potential range of species like *A. altissima* requires integration of all the above-mentioned factors (Cabra-Rivas et al. 2016) and the situation with *A. altissima* in South Africa provides a good study system for developing such an approach. It is interesting to examine the relative roles of climatic and other factors in shaping the potential distribution of *A. altissima* in South Africa, where the species – although having a long residence time in country – is yet to replicate similar levels of invasion success as it has in other parts of its adventive range. We address the following questions: (1) To what degree has *A. altissima* occupied its potential range in South Africa?; (2) Are there noticeable differences between the model outputs achieved through modelling the potential distribution of *A. altissima* at a global scale using coarse grain variables (10 arc-minute resolution), and modelling at a country scale using finer-grain variables (5 arc-minute resolution)?; (3) What are the most influential factors that determine the potential spread of *A. altissima* at a global and country scale?; (4) Which areas are at risk of future invasion by *A. altissima* in South Africa?

Methods

Study species

Ailanthus altissima Mill. Swingle (Simaroubaceae; tree of heaven) is a deciduous, dioecious tree species that is native to China. It has been widely planted globally and its adventive range now covers all continents except Antarctica (Kowarik and Säumel 2007). The species is a notorious invader in the northern hemisphere (Kowarik and Säumel 2007; Cabra-Rivas et al. 2016), but has yet to replicate such levels of invasion success in some other parts of the world, including South Africa. The species has several characteristics that are typical of successful invasive plant species, including prolific seed production (ca. 350 000 per female tree/year), rapid juvenile growth (Burch and Zedaker 2003), the ability to withstand harsh environmental conditions, including high levels of atmospheric pollution (Lawrence et al. 1991), and the ability to reproduce vegetatively after disturbance (Bory et al. 1991; Kowarik 1995; Kowarik and Säumel 2007; Constán-Nava et al. 2010). It is a popular ornamental plant in urban centres around the world and has also been widely used for

roadside restoration (Kowarik and Säumel 2007; Constán-Nava et al. 2010). In its adventive range *A. altissima* is most common and abundant in urban areas where it mainly occurs in disturbed sites, degraded fields, along roads and in riparian habitats (Kowarik and Säumel 2007; Constán-Nava et al. 2010). It is also invasive in many protected areas (Foxcroft et al. 2017). The first record of the species in South Africa is from 1834 (Bradlow 1965). Despite the fact that it has been in South Africa for a long time, it has not been widely disseminated until fairly recently. Because of the substantial impacts of this species to urban infrastructure (Celesti-Grapow and Blasi 2004; Kowarik and Säumel 2007) and human health (Vaz et al. 2017; Potgieter et al. 2017), strategic interventions to prevent its further spread in South Africa are needed.

Data collation

Distribution data for *A. altissima* were collected from many sources and compiled into a global database and a South African database. Global distribution data were taken from (1) the Global Biodiversity Information Facility (GBIF); (2) Centre for Agriculture and Biosciences International (CABI); (3) the Global Invasive Species Database (GISD); and (4) Delivering Alien Invasive Species Inventories for Europe (DAISIE). Distribution data for South Africa were obtained from (1) the South African Plant Invaders Atlas (SAPIA) database (see Henderson 1998); (2) the City of Cape Town's Invasive Species Unit; (3) the South African National Biodiversity Institute's (SANBI) Invasive Species Programme (ISP); (4) herbarium records; and (5) from the online biodiversity website iSpot (http://www.ispotnature.org/). Additional data points were collected during random searches in the Western Cape, Gauteng and KwaZulu-Natal provinces during 2015. An article in the popular South African magazine *Veld & Flora* (December 2015 issue) about the species yielded 12 new occurrence records.

Since the environmental data were obtained from different data sources and at different spatial resolutions, both data sets were resampled at the same grid size to match the occurrence data for each scale (10-arc minute resolution for the global scale; 5-arc minute resolution for the country scale). Data were edited by removing replicates, records without any co-ordinates, obviously erroneous records (e.g. in the sea) and those that appeared to be outliers. This was done using the *biogeo* package available in R (Robertson et al. 2016).

Climatic variables were obtained from the WorldClim database (Hijmans et al. 2005). All 19 variables were downloaded at 10-minute spatial resolution for the global model, and at 5-minute spatial resolution for the South African model. When compared against each other (using a correlation test), we determined a high level of multicollinearity between the WorldClim climatic variables that were downloaded at both spatial scales. The utilization of environmental variables that exhibit high

levels of multicollinearity is known to increase the appearance of errors in the final model output (Cruz-Cárdenas et al. 2014). Given the large number of climatic variables and the multi-collinearity among them, a principal component analysis (PCA) was performed at both spatial scales (Cabra-Rivas et al. 2016). For each of the first four axes (cumulative variation explained was >84%), variables accounting for the highest levels of variability were selected and used as climatic predictors. We selected the following climatic variables to account for variability at the global scale (in order of importance): mean temperature of the warmest quarter (Bio_10), temperature annual range (Bio_7), precipitation of the driest month (Bio_14), and mean temperature of the wettest quarter (Bio_8). At the country scale, the following climatic variables were selected: isothermality (Bio_3), temperature annual range (Bio_7), annual mean temperature (Bio_1) and precipitation of warmest quarter (Bio_18).

Land cover information was obtained from the GlobCover 2009 database for the global model (Arino et al. 2012), and from the 72 Class GTI South African National Land Cover Dataset (available at: http://bgis.sanbi.org/DEA_Landcover/project.asp) (DEA 2015) for the South African model. Categories were matched by grouping land-use data into six new categories for both the global and country models. We created similar land-use classes at both the global and country scales. However, since land-use data were from different sources, the final land-use classes differed slightly for the two spatial scales. For the global scale, we grouped the land-cover information from the GlobCover 2009 dataset into the following categories: (1) % built-up areas, (2) % agriculture, (3) % forest, (4) % mosaic vegetation, (5) % bare areas (no vegetation), and (6) % wetlands. These data were then aggregated to match a 10-minute spatial resolution. At the country scale, we categorized the land cover data as follows: (1) % human occupancy (urban and rural areas), (2) % agriculture, (3) % forest, (4) % mosaic vegetation, and (5) % bare areas (no vegetation). These data were then aggregated to match a 5-minute spatial resolution. All land-use classes at both spatial scales were used to develop species distribution models.

Human Footprint (HFP) data, which provides an index of anthropogenic impacts on the environment (Woolmer et al. 2008), were obtained from the SEDAC database (Sanderson et al. 2002) for both the global and country models. These data were then aggregated to match a 10-minute spatial resolution for the global scale, and a 5-minute spatial resolution for the country scale. HFP is a global dataset of 1-km grid cells created from nine global data layers that include human population pressure, human land use and infrastructure and human access. It indicates the degree of disturbance in the community ranging from 0 (wild) to 100 (highly disturbed) (Woolmer et al. 2008). For each model, the final set of explanatory variables included climatic, land use and human

footprint variables (Table 1). None of the environmental variables showed a Pearson correlation coefficients greater than 0.7.

Table 1 Final set of explanatory variables specifying the scale and data source used to develop the species distribution models at the global and country scale.

Variable type	Variable description	Scale	Data source
Climate	Precipitation of driest month [bio14]	Global	WorldClim database (Hijmans et al. 2005; http://www.worldclim.org/bioclim.htm) [A] (*A)
Climate	Mean temperature of warmest quarter	Global	*A
Climate	Mean temperature of wettest quarter	Global	*A
Climate	Temperature annual range [bio5-bio6]	Global, country	*A
Climate	Precipitation of warmest quarter	Country	*A
Climate	Isothermality [bio2/bio7] [*100]	Country	*A
Climate	Annual mean temperature [bio1]	Country	*A
Land use	% Agriculture	Global	GlobCover 2009 dataset (Arino et al. 2012; http://due.esrin.esa.int/page_globcover.php) [B]
Land use	% Bare areas	Global	*B
Land use	% Built-up areas	Global	*B
Land use	% Forests	Global	*B
Land use	% Mosaic vegetation	Global	*B
Land use	% Wetland	Global	*B
Land use	% Human occupancy (urban and rural)	Country	72 Class GTI South African National Land Cover Dataset (DEA Open Access, 2015) [C]
Land use	% Wetland	Country	*C
Land use	% Forest	Country	*C
Land use	% Agriculture	Country	*C
Land use	% Mosaic vegetation	Country	*C
Land use	% Bare areas	Country	*C
Disturbance	Human footprint	Global, country	SEDAC database (Sanderson et al. 2002; http://sedac.ciesin.columbia.edu/data/set/wildareas-

Modelling at a global scale

A set of ensemble models were built to characterize the full-range niche requirements for *A. altissima* at a global scale. A total of 3205 unique global occurrences for *A. altissima* encompassing both the native and non-native ranges of the species were used. The choice of algorithm influences the overall model output (Thuiller et al. 2004; Roura-Pascual et al. 2009; Cabra-Rivas et al. 2016). However, there is no single technique that is most affective at predicting potential species distribution (Pearson et al. 2006). Consequently, four algorithms were selected to model the potential global distribution of *A. altissima*. Two regression methods - Generalized Linear Models (GLM; Faraway 2016) and Multivariate Adaptive Regression Splines (MARS; Friedman 1991) - and two machine-learning methods- Random Forest (RF; Liaw and Wiener 2002) and Generalized Boosted Models (GBM; Ridgeway 1999) - were selected. All algorithms were implemented using the *biomod2* package (Thuiller et al. 2013) in R. All of the selected algorithms require presence-absence data to build models (Elith and Leathwick 2009), our global dataset included presence-only records. Barbet-Massin et al. (2012) found that models fitted with a large number of pseudo-absences that are equally weighted to the presences (i.e. weighted sum of pseudo-absences equals the weighted sum of presences) produced the most accurate predicted distribution models. They also found that fewer replicates were required when a larger number of pseudo-absence records were generated. Therefore, a single set of 10000 pseudo-absence records was generated (Barbet-Massin et al. 2012). Because presence-only data of alien species can suffer geographical biases due to dispersal limitation of the species, we restricted the selection of pseudo-absence points to the grid cells surrounding every presence (no further than four grid cells distance away from each presence) (Barbet-Massin et al. 2012). We thereby minimized commission errors in areas that may be suitable for the species but are not yet colonized (Cabra-Rivas et al. 2016). We implemented a split-sample cross-validation procedure where all models were calibrated on 70% of the initial data randomly selected, and evaluated on the remaining 30% (70-30 % split) with the area under the ROC curve (AUC; Fielding and Bell 1997; Cabra-Rivas et al. 2016). Ten cross validations were performed for each algorithm and pseudo-absence dataset resulting in a total of 40 different models being calculated for the species globally (one pseudo-absence dataset × four algorithms × ten replications). To improve the overall accuracy of SDM predictions, only models with an AUC score ≥ 0.8 were retained to build a committee-averaging ensemble model (Crossman and Bass 2008). A single output consisting of the percentage of agreement among models is created by utilizing this method (Gallien et al. 2012).

Modelling at a country scale

Presence records for *A. altissima* in South Africa were pooled from various databases and sources. Replicates and unreliable records were removed from the dataset using *biogeo* and a maximum of

one record was retained for each 5-minute grid cell. This left a total of 539 records. However, to ensure that testing took place on spatially separated blocks, we set a minimum distance of 30 km between each presence record, thereby avoiding biases associated with over sampling in certain areas and ensuring the accuracy of the final model output. This further reduced the total number of unique records to 90. Pseudo-absences were selected in a way that both minimized the sampling biases from the occurrence data (Phillips et al. 2009) and accounted for the dispersal limitations of the species in South Africa (Gallien et al. 2012). As a first step, we mitigated biases due to dispersal limitations by selecting pseudo-absences within the vicinity of any of the presence records (no more than four grid cells distance from each presence record; Cabra-Rivas et al. 2016). Then, as a second step, we used the predictions of the global models to attribute weights to our pseudo-absences as a way of avoiding contingent absences. Weights ranged from 0 (low probability of being a true absence) to 1 (high probability of being a true absence) (for further details see Gallien et al. 2012). 1836 pseudo-absence records were selected to represent all areas surrounding each presence records. We used the same four statistical algorithms applied for the global model, followed by 10 cross-validation repetitions. This resulted in a total of 40 models being developed for the species in South Africa (one pseudo-absence dataset × four algorithms × ten replications). The same split-sample cross-validation procedure was used as in the global model (70-30%). To avoid a false inflation of AUC measures due to spatial autocorrelation, a filtering point approach was selected (Marcer et al. 2012). A filtering point approach sets a minimum spatial and environmental distance between occurrences and examines these for residual autocorrelation (Marcer et al. 2012). The smaller number of species occurrences together with the high restrictions imposed on pseudo-absence selection lead to a decrease in AUC scores (Lobo et al. 2008). Only models with AUC scores ≥ 0.7 were retained to build the committee-averaging ensemble model.

Statistical analyses

The relative importance of each of the selected variables was determined at both spatial scales. A confusion matrix was produced showing: 1) the number of points predicted as suitable by both the global and country models; 2) the number of points predicted as suitable by either the global or the country models; and 3) the number of points predicted as unsuitable by both the global and country models (Fielding and Bell 1997). Using the values obtained from the confusion matrix, the true skill statistic (TSS), as well as the sensitivity and specificity values were calculated (Fielding and Bell 1997; Allouche et al. 2006). TSS, a measure of predictive accuracy that is independent of prevalence (Allouche et al. 2006), was used to estimate the level of agreement between the global and country-level model predictions. TSS integrates sensitivity and specificity values into a single metric, and is calculated with the following formula: TSS = (sensitivity + specificity)-1. In this context, sensitivity

refers to the proportion of presences predicted by the global model that are also predicted present by the country model, whereas specificity refers to the proportion of absences predicted by the global model that are also predicted absent by the country model. These metrics (TSS, sensitivity and specificity) are usually used to quantify model performance by comparing the model predictions to independent presence and absence records. In this study, however, they are used to indicate agreement between the global and country model, and thus do not indicate model performance.

Results

Relative importance of distribution drivers

Cumulatively, climate variables (50.8%) were the most influential drivers affecting the distribution of *A. altissima* at the global scale. This was followed by land use (33.8%) and human-mediated disturbances (15.5%). In contrast, at the country scale human footprint (51.1%) was the most influential driver, followed by land use (30.0%) and then climate (18.9%) (Fig. 1a).

Individually, percentage of built-up areas (18.3%) and temperature annual range (17.4%) were the most influential variables at the global scale, followed by the mean temperature of the warmest quarter (16.3%) and human-mediated disturbances (15.4%) (Fig. 1b). At the country scale, human-footprint (51.1%) was the most influential variable affecting *A. altissima* distribution, followed by the land-use category - percentage human occupancy (20.9%). Isothermality (mean diurnal range/temperature annual range) (7.3%) and temperature annual range (4.7%) were the two most influential climatic variables at the country scale (Fig. 1c).

The response curves indicate how the four algorithms used in the models predict the way in which the species responds to these variables. At the global scale, all model algorithms show similar responses and indicate that *A. altissima* tends to occur: in highly built-up areas (Fig. 2a), in regions of high human footprint (Fig. 2d) and of low annual range in temperature (Fig. 2b). It also appears that the species tends to occur more in regions hosting intermediate values of mean temperature during the warmest quarter of the year (although these curves reveal partial disagreement between algorithms; Fig. 2c). Similarly to the results of the global scale, at the country scale the species tends to occur more frequently in sites of high human footprint (Fig. 2e), and high human occupancy (Fig. 2f).
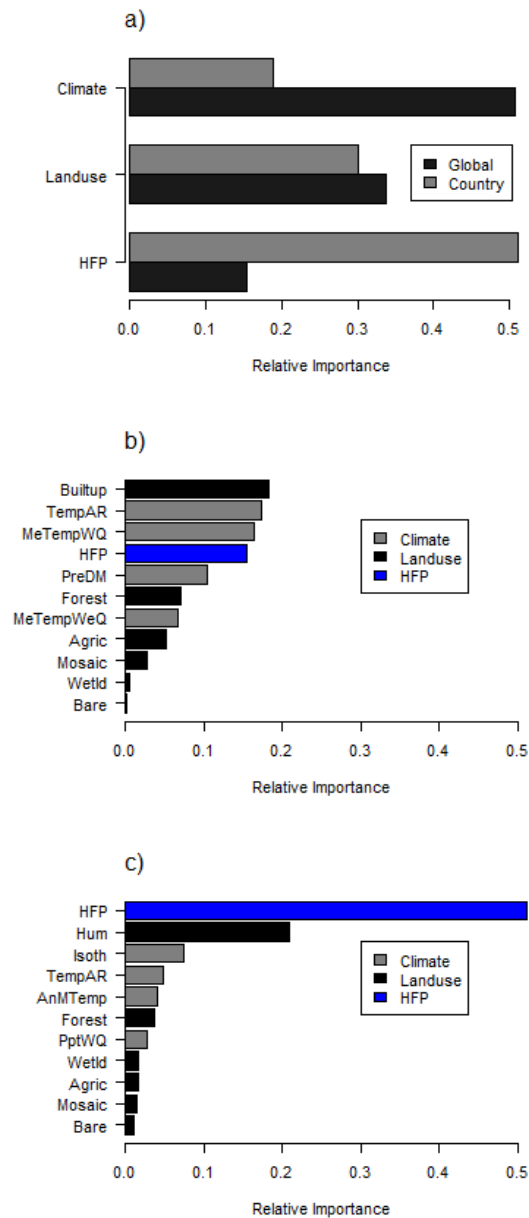
Fig. 1 Relative importance of the variables for predicting the distribution of *Ailanthus altissima* for both the global and country models for **a)** variables grouped into three classes, b) for individual variables in the global model, and c) for individual variables in the country model. Variables: Built-up = % built-up areas; TempAR = temperature annual range; MeTempWQ = mean temperature of the warmest quarter; HFP = human footprint; PreDM = precipitation of the driest month; Forest = % forests; MeTempWeQ = mean temperature of the wettest quarter; Agric = % agricultural areas; Mosaic = % mosaic vegetation; Wetld = % wetlands; Bare = % bare areas;Hum = % human occupancy; Isoth = isothermality; AnMTemp = annual mean temperature; PptWQ = precipitation of the warmest quarter.
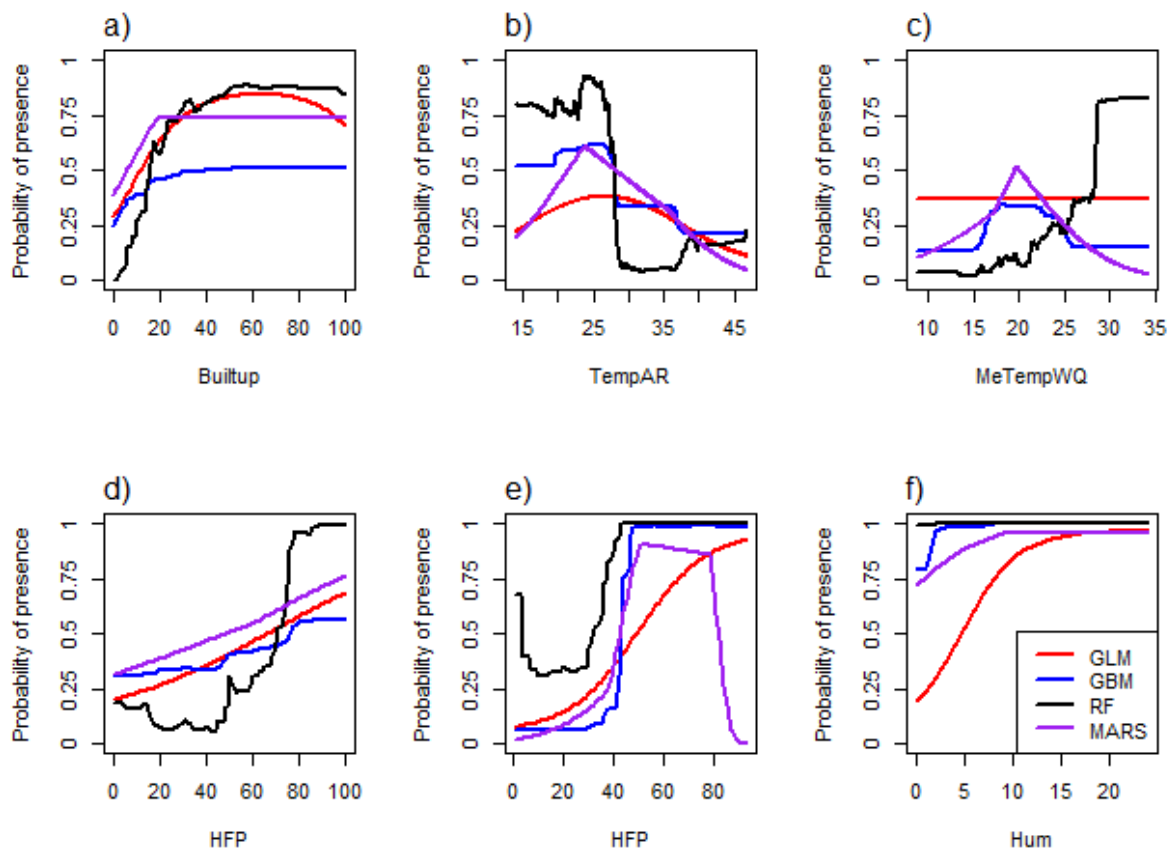
Fig. 2 Changes in *A. altissima* along environmental gradients as predicted by the (a-d) global and (e-f) country level models. The response curves show species response to the main predictors of the global (Builtup, TempAR, MeTempWQ, HFP) and regional models (HFP, Hum), as estimated by the four algorithms: Generalised Linear Model (GLM; red line), Generalised Boosted Regression (GBM; blue line), Random Forest (RF; black line), and Multivariate Adaptive Regression Splines (MARS; purple line). Variables: Builtup = % built-up areas, TempAR = temperature annual range (in °C), MeTempWQ = mean temperature of the warmest quarter (in °C), HFP = human footprint index, Hum = % human occupancy.

Degree to which Ailanthus altissima *has occupied its potential range, and risk maps*

Within South Africa, *A. altissima* is widespread and abundant throughout the province of Gauteng, where the country's largest city, Johannesburg, is situated (Fig. 3). Projections from both the global and country models predicted presences in most grid cells throughout this province (Fig. 4). The species is fairly widespread in the southwestern part of the Western Cape, especially in and around the cities of Cape Town and Knysna. The species has a scattered distribution in parts of the Eastern Cape, Free State and Mpumalanga. Both the global and country-scale models predicted presences in grid cells corresponding with the major cities of South Africa, including Johannesburg, Cape Town,

Durban, Port Elizabeth, East London, Nelspruit and Bloemfontein. Global-scale model projections predicted presences in all of the provinces, but only very few suitable cells in the arid Northern Cape Province. The country-scale model also predicted suitable cells in all provinces but identified more high-suitability cells across the country than the global model. Both country- and global-scale models predicted presences in grid cells surrounding Durban, where there are currently no records of *A. altissima* occurrence (Fig. 5).
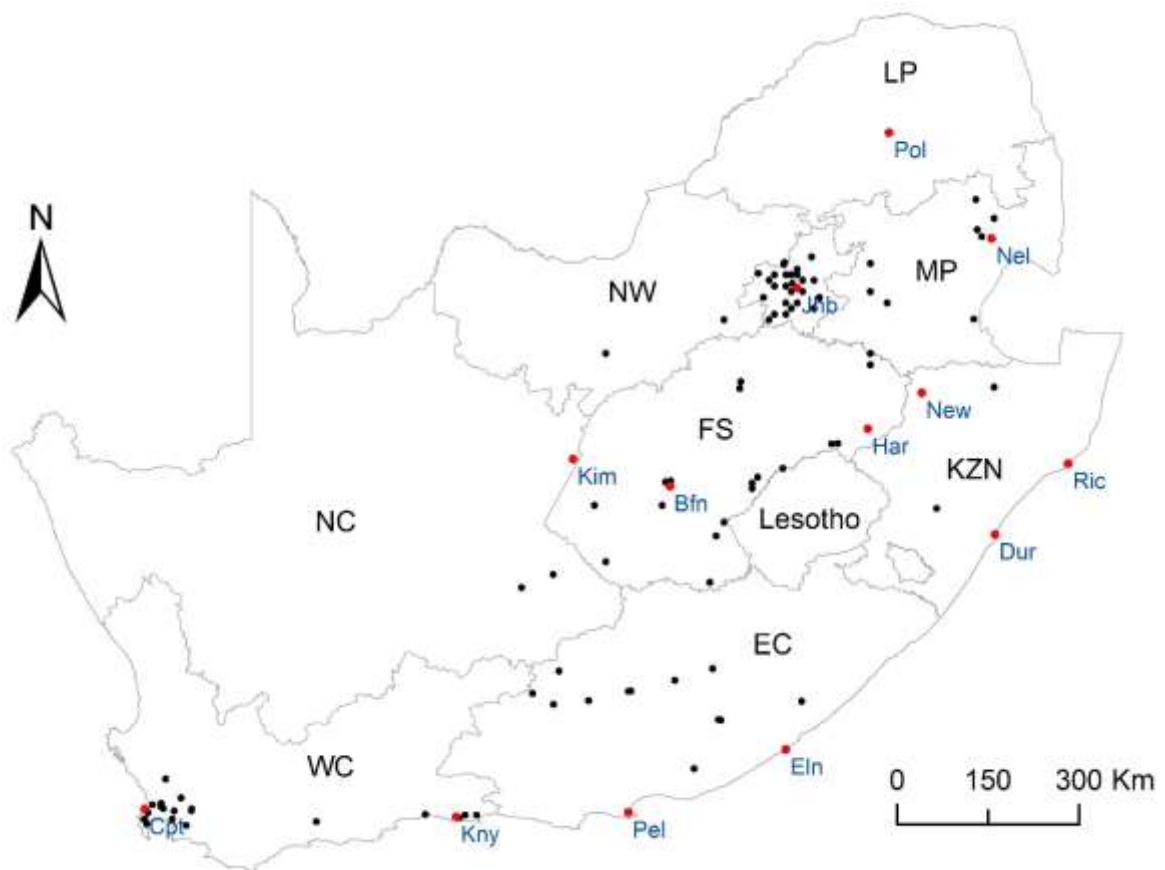
Fig. 3 Current distribution of *Ailanthus altissima* in South Africa. Provinces (WC = Western Cape; EC = Eastern Cape; KZN = KwaZulu-Natal; MP = Mpumalanga; LP = Limpopo; GP = Gauteng; FS = Free State; NW = North West; NC = Northern Cape) and selected cities (Cpt = Cape Town; Kny = Knysna; Pel = Port Elizabeth; Eln = East London; Dur = Durban; Ric = Richards Bay; Har = Harrismith; New = Newcastle; Kim = Kimberly; Bfn = Bloemfontein; Jhb = Johannesburg; Nel = Nelspruit; Pol = Polokwane) are shown in red dots.
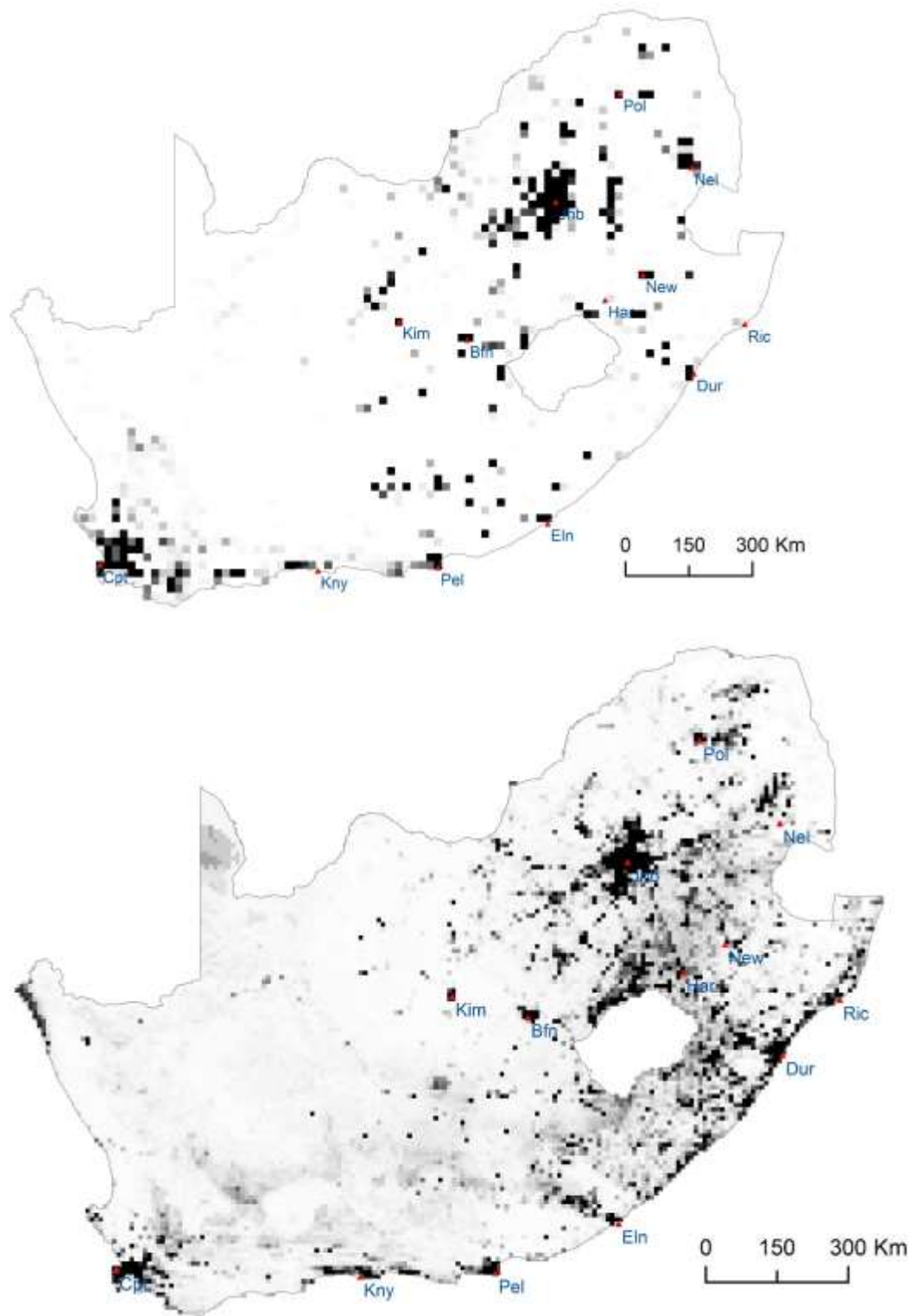
Fig. 4 Maps showing areas predicted suitable for *Ailanthus altissima* in South Africa in global-scale (**top**) and country-scale models (**bottom**). Black shading indicates highly suitable areas; shades of grey indicate less suitable areas; unshaded areas are unsuitable for the species. Cities in which *A. altissima* is abundant (Cpt = Cape Town; Kny = Knysna; Pel = Port Elizabeth; Eln = East London; Dur = Durban; Ric = Richards Bay; Har = Harrismith; New = Newcastle; Kim = Kimberly; Bfn = Bloemfontein; Jhb = Johannesburg; Pol = Polokwane; Nel = Nelspruit) are shown as red dots in both figures.

14
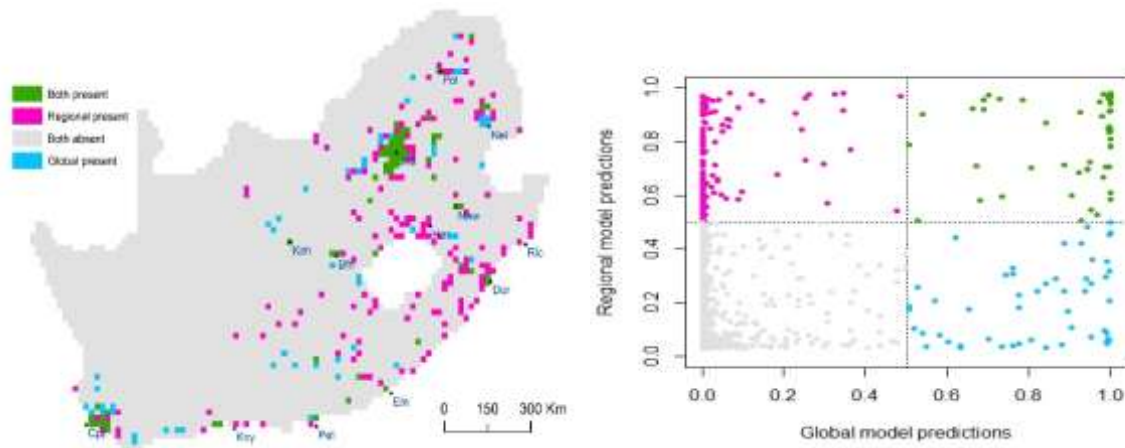
Fig. 5 Combined model output and confusion matrix showing areas predicted to be suitable for *Ailanthus altissima* in both the global- and country models (*green*), areas that are predicted as suitable by just the global model (*blue*) or country model (*pink*) and areas that are predicted as unsuitable by both the global- and country models (*grey*).

The global model identified approximately 3% of South Africa as being suitable for the species, whereas the country-scale model predicted approximately 6% of South Africa as suitable. There was a reasonable agreement in the predictions between the two models (Fig. 5). Sixty-five cells (out of a total of 3941 cells across South Africa) were identified as being suitable for the species by both models (ca. 1.5%). The country-scale model predicted 155 cells (3.9%) to be suitable that were not predicted to be suitable by the global model. These cells are scattered throughout the central part of South Africa (including Free State and Eastern Cape provinces) and along the coast of the Eastern Cape and KwaZulu-Natal. Fewer cells (52; 1.3%) were predicted to be suitable by the global model but not by the regional model. Overall, the global and country-scale models identified broadly similar regions as being potentially suitable for this species. The most important difference between these predictions is the large number of cells in the Eastern Cape and KwaZulu-Natal provinces predicted to be suitable by the country-scale model but not by the global model. Both models suggest that the species is capable of surviving across a broad range of climatic conditions. The sensitivity was 0.55, specificity was 0.96, and True Skill Statistic was 0.52.

Discussion

Relative importance of predictor variables

The potential distribution of invasive species is influenced by many factors whose relative importance varies according to spatial scale (Rouget and Richardson 2003; Guisan and Thuiller 2005;

McGill 2010; Cabra-Rivas et al. 2016). Factors such as climate (Hijmans and Graham 2006; Hellman et al. 2008), land use (McKinney 2008) and anthropogenic effects (Hulme 2009) clearly have important effects on the distribution of invasive species globally. This study (and others; see Guisan and Thuiller 2005; Gallien et al. 2010; Cabra-Rivas et al. 2016) highlights the importance of incorporating these multiple factors into models to determine the potential range of an invasive species. Our analysis showed that climatic factors were most important for explaining range limits of *Ailanthus altissima* at the global scale. This result is in line with several other studies that concluded that, at a global scale, climate has the greatest effect on the broad range limits of invasive species (see Hellman et al. 2008; Jeschke and Strayer 2008). The next most important factors for explaining *A. altissima* distribution globally are land use and then human-mediated disturbance. At a national scale, for South Africa, human-mediated disturbance (human footprint and percent human occupancy) were the most influential drivers of *A. altissima* distribution. The current distribution of the species in South Africa coincides with large cities and towns, suggesting that the historical planting of the species occurred in urban and suburban areas. *Ailanthus altissima* has spread throughout its adventive range due to its introduction and dissemination as an ornamental plant in urban settings (Kowarik and Säumel 2007), and the species is still most common and abundant in cities and towns. The first record of *A. altissima* in South Africa is from Cape Town in 1834 (Bradlow 1965), but very little is known about the subsequent history of dissemination and spread of the species throughout the country. Female trees were clearly selected for cultivation in urban areas in preference to male trees because the flowers of male trees emit a foul-smelling odour. The regeneration biology of the species in South Africa has not been studied but it is likely that the preference of female trees in plantings has increased seed production, ultimately promoting the spread of the species.

Relevant determinants of species distribution

Although *A. altissima* tolerates a wide range of climatic conditions, it is most common and abundant in temperate climatic zones (Knapp and Canham 2000; Kowarik and Säumel 2007; Clark et al. 2014). The climatic variables that were identified as key drivers were consistent with the climatic requirements reported in the literature (see Kowarik and Säumel 2007). In agreement with the findings of Cabra-Rivas et al. (2016), we found that at the global scale, the distribution of *A. altissima* is characterized by intermediate temperature conditions. Invaded areas experience warm temperatures during the day (21°C - 27°C) that drop slightly at night (13°C - 18°C) with extreme fluctuations seldom being recorded (Shaver et al. 2000). Cabra-Rivas et al. (2016) found annual mean temperature to be the most influential distribution driver at the global scale (35.3%) whereas we found the percentage of built-up areas to be the most influential variable (18.3%), closely followed

by temperature annual range (17.3%) and mean temperature of the warmest quarter (16.3%). Precipitation also influenced the distribution of the species at the global scale (precipitation in driest month, 10.4%); although *A. altissima* is fairly drought tolerant, it does not grow well in areas with pronounced droughts (Albright et al. 2010). This could explain why it is not predicted to occur in the most arid province, the Northern Cape, although this province also has a low human population density with few large urban areas (low human footprint). In contrast, at the country scale, human footprint (51.1%) and the percentage human occupancy (20.9%) were the most important environmental predictor variables, and had a combined contribution of more than 70%.

At both global and country scales the percentage of built-up or human occupied areas, and zones with high levels of human-mediated disturbance (human footprint indicator) have a large influence on the distribution of *A. altissima*. A high level of human influence is linked to high propagule pressure (Cabra-Rivas et al. 2016) which has likely facilitated the spread and establishment of this species in its adventive range. This high human footprint (human-mediated disturbances) in conjunction with the anthropogenic influences that are characterised by various transportation pathways and dispersal corridors in built-up areas have clearly acted as efficient mechanisms for promoting the spread of *A. altissima* throughout urban ecosystems in South Africa. This agrees with findings from other parts of the world where *A. altissima* is most common and abundant in urban areas (Huebner 2003). It is therefore not surprizing, human influences have a large effect on the distribution of this species in South Africa.

In summary, we conclude that *A. altissima* tolerates of a broad range of climatic conditions and that high levels of human-mediated disturbances are particularly important drivers of the distribution of this species at both a global and a country scale.

Degree to which the potential range has been occupied, and risk maps

Many areas identified as being suitable for *A. altissima* occurrence in South Africa already have established populations, but some uninvaded areas appear to be suitable for this species. As the species appears to invade urban areas, further extensive spread into natural areas is not expected under current climatic conditions. Further spread of the species in the Eastern Cape and KwaZulu-Natal provinces is likely. In particular, the city of Durban and other urban areas along the coast between this city and Richards Bay are likely to be invaded in the future, as are cities such as Port Elizabeth and East London in the Eastern Cape. Increases in population density in and around urban centres areas where the species is already established is inevitable in the absence of management.

Although the global and country models show reasonable agreement (number of grid cells where presences were predicted by both the global and country model = 65; number of grid cells where absences were predicted by both models = 3669), there are certain areas that are identified as suitable only by either the global (number of grid cells where presences were predicted by only the global model = 52) or country-scale models (number of grid cells where presences were predicted by only the country model 155). Areas that were identified as suitable in the country model but not in the global model could be because of the coarseness of the environmental variables that were used (Guisan et al. 2007). It is clear that 5-minute spatial resolution cells had generally higher human footprint values compared with corresponding 10-minute cells containing South African presence records (Fig. 6). As the human footprint variable has been shown to be particularly influential in limiting the distribution of the species (Fig. 1), many of the 5-minute cells were identified as being potentially suitable for the species due to high human footprint values (country model) but due to the generally lower values for many corresponding 10-minute cells (global model) these cells were predicted to be less suitable. The difference in human footprint values could occur because one of the four 5-minute cells nested within a 10-minute cell has a high human footprint value while the other three have low values, resulting in a lower overall value for the 10-minute cell.
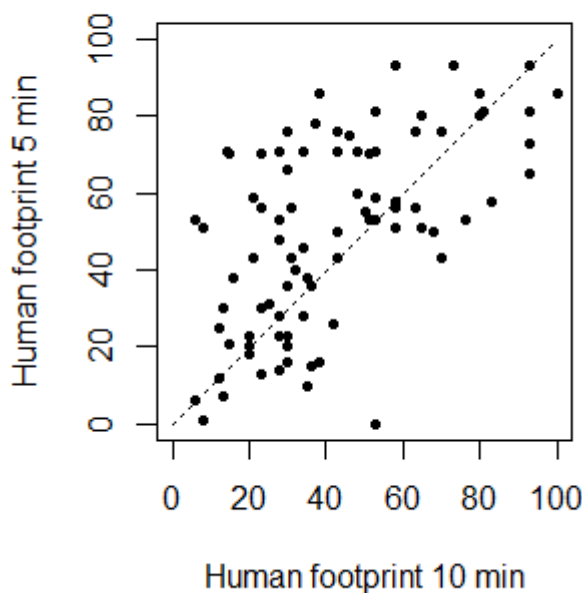
Fig. 6 Human footprint values associated with South African presence records for *Ailanthus altissima* that were extracted from the 5-minute and 10-minute spatial resolution human footprint predictor variable map.

Our model comparison yielded a higher specificity value (Sp = 0.95) compared to the sensitivity value (Sn = 0.56). This suggests that our projected model outputs were largely in agreement about where absences (95%) were predicted. Most of South Africa is not suitable for invasion by *A. altissima*, so this high specificity value makes sense. The lower sensitivity scores indicate that our global and country-scales models were only partly in agreement regarding where predicted presences for the species may occur. The greater number of cells predicted as being suitable by the country model than the global model largely explains the relatively low sensitivity. These differences between the two models may partly be explained by the different weight they attributed to the human footprint variable. As sensitivity influences the True Skill Statistic, a relatively low TSS value (TSS = 0.52) results from the relatively low sensitivity value.

Management of A. altissima in South Africa

In South Africa, the country model predicts that most of the urban areas in South Africa are suitable for *A. altissima.* The species has a broad climatic range and climate does not appear to have a major role in shaping the distribution of the species in South Africa. Considering the areas already invaded in South Africa, it is clear that the species can survive and flourish in a wide range of climatic conditions, from a Mediterranean-type climate in the Western Cape (Cape Town) to a highly seasonal environments with summer rainfall in the central regions of the country (e.g. Bloemfontein). It can survive cold winters (e.g. Bloemfontein and eastern Free State Province) and warm humid conditions, as indicated by records around Nelspruit in the subtropical Lowveld on the eastern border of South Africa. Towns and cities where this species is likely to be able to survive but where it has yet to be recorded include Durban, Richards Bay, Port Elizabeth, East London, Kimberley and Polokwane. For most of these cities, both the global and country models predict high environmental suitability. If this species has not reached these cities (as suggested by the occurrence records used in this study) then early-detection and rapid-response plans should be developed for these cities. Another region where the species is predicted to be able to invade is along the eastern coastal region between just south of Durban and Richards Bay. This area has many coastal towns and villages where disturbance and thus human footprint is high. Similarly, this region should be prioritised for early detection and rapid response.

Species distributional models, especially when the roles of a range of climatic and other factors are explicitly assessed (as was done in this study), can assist in identifying areas where early detection, rapid response (EDRR) initiatives and other management efforts should be implemented. Containment and reducing the size of established *A. altissima* populations nationally will limit further spread and impacts (Wilson et al. 2007). EDRR initiatives in areas with low densities of *A.*

altissima will improve the possibility of species eradication with follow-up control measures preventing future re-establishment of the species. Methods for producing risk maps to guide such operations were proposed for another emerging invasive tree species in South Africa (*Acacia stricta*; Kaplan et al. 2014) and a similar approach could be applied for *A. altissima*. Insights from this study provide a starting point for the development of a national-scale strategic plan for managing *A. altissima*, along the lines of plans developed for other invasive trees in South Africa (e.g. van Wilgen et al. 2011; Shackleton et al. 2017).

Conclusions

Effective management of invasive species requires the accurate assessment of the potential geographical range of the invaders and an understanding of the factors that promote their spread. This study indicates that although *A. altissima* can spread further in South Africa, extensive spread throughout the country is very unlikely, given the species' preference for urban conditions. Delimiting potential areas of invasion in relation to current areas of establishment ultimately reduces management costs. We found distinct differences in the model outputs at global and country scales, with climate being the prevailing factor influencing the spread of the species globally, whereas factors relating to human-mediated disturbances were most influential explanatory variables at the country scale. This study highlights the importance of incorporating different environmental variables at various spatial scales to identify areas of high invasion potential. This multi-scale approach facilitates the early detection of invaders ultimately preventing their spread and introduction into high-risk areas.

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