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On the present and potential distribution of *Ageratina adenophora* (Asteraceae) in South Africa

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ABSTRACT

Invasive alien plants pose a threat to biodiversity worldwide, and the costs of control are ever-escalating. Early detection and prediction of areas potentially at risk is crucial to minimise ecological and socio-economic costs. Maxent was used to predict the area within which *Ageratina adenophora* can potentially naturalise and spread in South Africa. The model was set up with 1020 occurrence records (10 replicates, 70% of records for calibration:30% for validation), and four climatic predictor variables. Background data were selected using Köppen–Geiger (vegetation-based) climate classification zones. All model replicates performed better than random in both binomial tests of omission and ROC analysis. The model was statistically significant and its mean AUC was 94%. The modeled prevalence was 0.21 and the sensitivity was 0.99. The Eastern Cape, KwaZulu-Natal, Mpumalanga and Gauteng provinces have climatic conditions indicative of a high potential for invasion by *A. adenophora*, followed by parts of the Western Cape, North West and Limpopo provinces. The model predicted areas beyond the current distribution, suggesting that *A. adenophora* has potential for further spread, and that searches for it need to be made beyond its currently known distribution. On the other hand it appears not to have spread into some climatically suitable areas near its current occupancy sites, such as throughout the KwaZulu-Natal mist belt, suggesting that unknown biotic (including human) or abiotic factors are also limiting its naturalization and require further study to be identified.

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1. Introduction

Invasive alien plants (IAPs) have been recognised as one of the drivers of global change (Kriticos et al., 2003; Mack et al., 2000), causing significant negative ecological and socio-economic impacts (Bradley, 2012; Papes and Peterson, 2003; Pimentel et al., 2005; Sheng, 1998). Plant invasions have been associated with declines in native biological diversity and, in some cases, complete transformation of whole landscapes (Gaertner et al., 2009; Richardson et al., 2000; Tererai et al., 2013; Vilà et al., 2011), and high costs of management (Starfinger et al., 2003). South Africa is among the countries that have the greatest problems with IAPs worldwide (Richardson and van Wilgen, 2004; Trethowan et al., 2011). Managers and policy makers require a synoptic view of biological invasions as early as possible in order to assess impact risks (Kriticos et al., 2003; Wang and Wang, 2006), thereby reducing costs of reactive management (Wang and Wang, 2006). Species

distribution modeling (SDM) facilitates early detection and rapid response (Richardson and van Wilgen, 2004).

Ageratina adenophora (Spreng.) R.M. King and H. Rob., previously known as *Eupatorium adenophorum* Spreng., is a weedy perennial shrub native to Mexico, and can grow up to 3 m in height (Heystek et al., 2011; Kluge, 1991; Sun et al., 2004; Wang and Wang, 2006). Several ecological attributes encourage its invasiveness. It is an extremely aggressive competitor especially in shaded conditions (Zhang et al., 2008; Zheng et al., 2009). A typical plant can produce up to 10,000 seeds per season, 70% of which are viable (Parsons and Cuthbertson, 1992) and can disperse over long distances (Wang et al., 2011) enabling it to invade rapidly. Large quantities of easily dispersible seeds make it more likely that environmental constraints rather than dispersal limitation control distribution (Syfert et al., 2013). Its seeds are long-lived, allowing large and persistent soil seed banks to develop rapidly (Shen et al., 2006). It suppresses biodiversity (Niu et al., 2007), reduces pasture carrying capacity and is poisonous to horses (Muniappan et al., 2009; Wang, 2005). The plant is allelopathic (Yang et al., 2008; Zheng and Feng, 2005; Zhong et al., 2007) and has been recorded as altering soil microbial communities in its favor (Niu et al., 2007; Yu et al., 2005). Stems set roots upon contact with the ground, facilitating the formation of dense stands (Muniappan et al., 2009; Sun et al., 2004).

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Globally, *A. adenophora* is invasive in southern and south-eastern Asia, eastern Australia, New Zealand, and South Africa (Cronk and Fuller, 1995; Kluge, 1991; Wang and Wang, 2006). In many of these countries, it invades crop fields, plantations, and pastures (Kluge, 1991). It prefers moist conditions, such as the edges of slow flowing streams and waterlogged sites on steep slopes in high rainfall areas (Heystek et al., 2011). China is one of the worst hit countries, with *A. adenophora* classified as one of their worst invasive alien species (Wang and Wang, 2006; Zhang et al., 2008). In South Africa, the first record of *A. adenophora* was from Limpopo province in 1958 (Heystek et al., 2011). *A. adenophora* is also naturalised in parts of the Western Cape, Mpumalanga, North-West and Gauteng provinces (Henderson, 2007; Heystek et al., 2011), but was expected to be most invasive in the mist-belt region of KwaZulu-Natal, where it is a weed of roadsides, railway embankments, riverbanks and commercial timber plantations around Pietermaritzburg (Kluge, 1991). In the Western Cape and North-West it appears to be restricted to riparian habitats, elsewhere it is also invasive in grasslands or forest margin habitats especially when these are disturbed as noted above. Globally, biological and chemical approaches have been used to control it, but with limited success (Wang and Wang, 2006; Zhang et al., 2008). In South Africa, a stem-galling tephritid fly (*Procecidochares utilis* Stone) and a leaf spot fungus (*Passalora ageratinae* Crous & A.R. Wood) were established in the 1980s, but with little apparent effect on the size and density of existing stands of *A. adenophora* (Buccellato et al., 2012; Kluge, 1991).

Predictive modeling of geographic distributions of species has many applications in analytical biology including management of IAPs (Phillips et al., 2006). In areas where *A. adenophora* has been invasive, much research has focused on its local pernicious effects and chemical control (Jiang et al., 2008; Yang et al., 2008; Yang et al., 2006). However, in China, several studies have investigated potential distribution of the species, using various modeling methods (Lu and Ma, 2006; Papes and Peterson, 2003; Sang et al., 2010; Wang and Wang, 2006; Zhu et al., 2007). Numerous methods exist to model species distributions where presence-absence data are available, but presence-only methods have been developed in recent decades (Yackulic et al., 2013). Commonly used presence-only methods include Genetic Algorithm for Rule-set Production (GARP) and Maximum entropy modeling (Maxent, Phillips et al., 2006; Phillips and Dudík, 2008). The authenticity of any presence-only model output is dependent on the degree to which its assumptions are met, among them randomized or representative sampling, and constancy of detection probability across sites. Accuracy of the predicted potential range also depends on a sufficiently large number of occurrence points, minimal sampling bias and the use of functionally relevant predictors (Dudík et al., 2007; Elith and Leathwick, 2009). We chose to use Maxent for several reasons including its successful use for many applications with presence-only data (Kumar and Stohlgren, 2009; Trethowan et al., 2011; Wolmarans et al., 2010), its better performance compared to other presence-only models (e.g. GARP) (Elith et al., 2006; Merow et al., 2013; Phillips et al., 2006; Trethowan et al., 2011), and that it has a concise mathematical algorithm and a well-understood statistical interpretation (Phillips et al., 2006; Yackulic et al., 2013). Furthermore, presence-absence data are rarely available and where available, are often of poor quality (Elith et al., 2006; Trethowan et al., 2011). Maxent is among the best performing modeling methods (Dudík et al., 2007).

While *A. adenophora* is an aggressive invader in other parts of the world (Heystek et al., 2011), especially Hawaii, China, New Zealand and Australia, it has not been as invasive as expected in parts of South Africa (Kluge, 1991). Despite this, *A. adenophora* remains a potential risk because it has had significant ecological effects where it has been a successful invader. Several reasons, although speculative, have been proposed for the rather slow rates of spread in South Africa, including the lack of a suitable climate and the effect of biological control agents that were released about three decades ago (Heystek et al., 2011). This study aims to identify the areas climatically suitable for naturalization

and possible spread of *A. adenophora* in South Africa. The specific question we ask is, “is the climate in South Africa suitable for invasion by *A. adenophora*?” The findings of this study will assist environmental managers to assess risk of *A. adenophora* spreading from present localities to non-invaded areas.

2. Materials and methods

2.1. Occurrence and “absence” records

We collected about 4000 occurrence records from online databases, namely the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>) and South African Plant Invaders Atlas database (SAPIA, Henderson, 2007). Most of the data records were museum and herbarium specimens that rarely arise from random or systematic sampling, necessitating the application of methods that minimise sampling bias (Elith et al., 2006; Pearce and Boyce, 2006; Yackulic et al., 2013). We checked the dates of collection (excluded records collected prior 1950 to match bioclim data—1950–2000), completeness of coordinates (at least one decimal place), coordinate precision (not more than 10 km), and excluded records from managed environments (botanical gardens and residential areas). Duplicates and any points falling in the oceans were removed. We allowed only one sample per 5-min pixel for calibration to avoid pseudo-replication, thereby minimising sampling bias (Phillips et al., 2009; Webber et al., 2011). The final occurrence dataset was mapped and overlaid on satellite images available on Google Earth (<http://www.earth.google.com>) to check if there were any artificial tendencies (e.g. points only occurring in accessible areas), and if the given habitat descriptions matched reality. We subsampled 50% of the remaining 2040 records by allocating random numbers, in order to reduce the risk of spatial autocorrelation. The data cleaning reduced the number of available records to a total of 49 in the native range and 971 in the invaded range, occurring across 13 countries. The use of data from both native and invaded range is important to capture the full range of climate conditions to which the species has adapted (Broennimann and Guisan, 2008). For “absence” data, Maxent relies on a user-defined geographical background of a reference set of grid cells which is compared to the climate of grid cells where the species is present (Webber et al., 2011). The selection of background (pseudo-absence) data significantly influences model results (Elith et al., 2011) and these were chosen using a non-arbitrary method. A subsample of 10,000 background points (recommended by Barbet-Massin et al., 2012) was randomly selected from a target group sample of 300,000 occurrence points across 300 species in the Asteraceae family. The background points were chosen such that they occur within the Köppen–Geiger climate zones in which presence of *A. adenophora* points occurred (Webber et al., 2011). We excluded all zones in which no presence of *A. adenophora* occurred, in order to make the background a better approximation of actual absences.

2.2. Predictor variables

Based on previous habitat modeling studies of *A. adenophora* (Papes and Peterson, 2003; Wang and Wang, 2006; Zhu et al., 2007) and those of other plant species in South Africa (Beaumont et al., 2005; Trethowan et al., 2011), we selected variables that are thought to be of biological relevance to its distribution (Kumar and Stohlgren, 2009). These included mean annual temperature (Bio1), mean diurnal temperature range (Bio2), temperature seasonality (Bio4), mean temperature of the coldest quarter (Bio11), annual precipitation (Bio12), precipitation of the driest month (Bio14), precipitation seasonality (Bio15) and precipitation of the wettest month (Bio13). We obtained these bioclimatic variables from the Worldclim database (Hijmans et al., 2005; <http://www.worldclim.org/bioclim.htm>), at 5-min spatial resolution suitable for capturing steep climatic gradients (Webber et al., 2011). We examined all variables for multicollinearity (Kumar

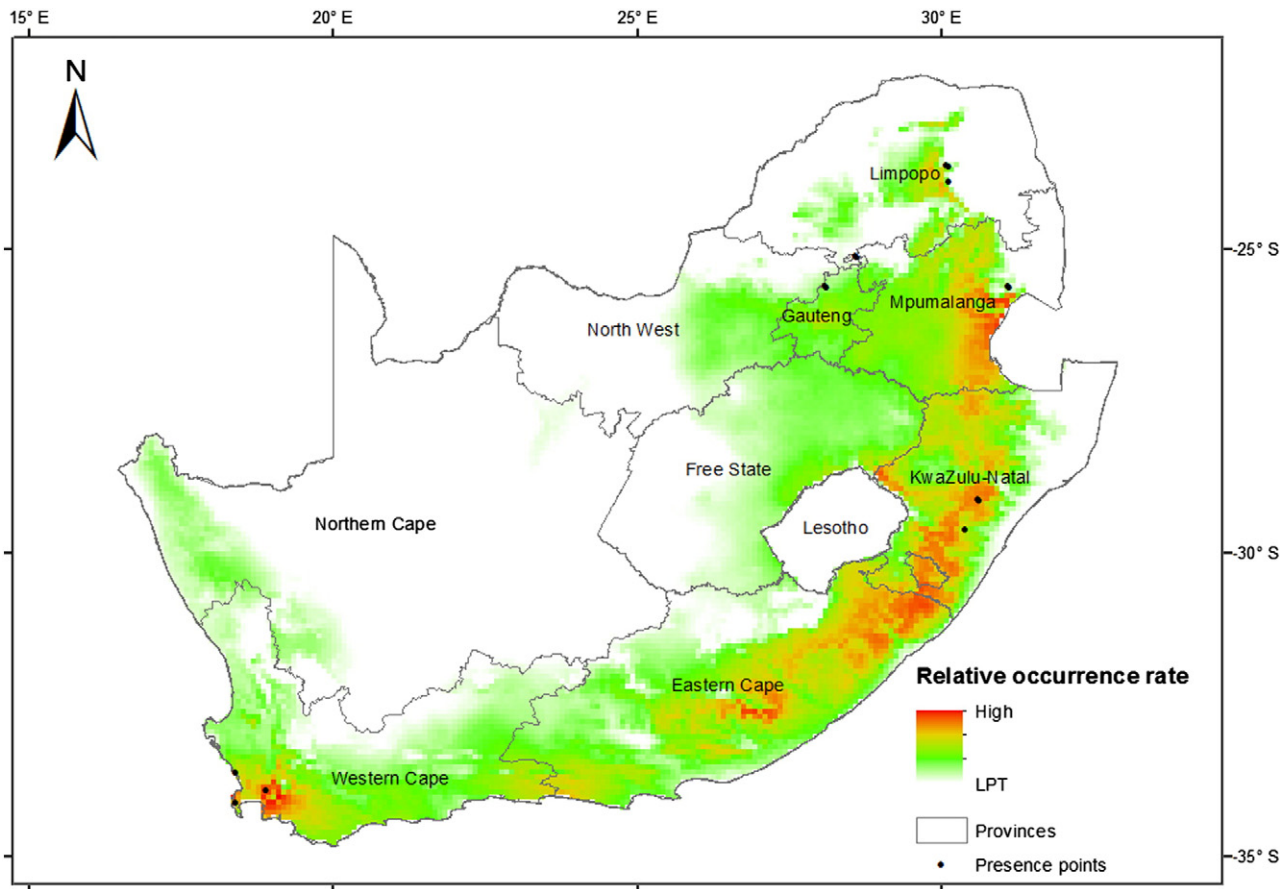


Fig. 1. Potential distribution of *Ageratina adenophora* in South Africa (average of 10 random models). The colors show relative suitabilities of different localities in South Africa for occupancy by *A. adenophora*. LPT is the lowest presence threshold. The black points are the current occurrence localities of *A. adenophora*.

and Stohlgren, 2009), after which we retained four (Bio1, Bio4, Bio12 and Bio15) that were least correlated ($-0.2 < r < 0.4$). The rest were strongly correlated ($r > 0.8$) with at least one of the four selected variables, or among themselves, thus were excluded for easy interpretation of results including modeled relationships and variable importance. Precipitation and temperature have long been recognized as major determinants of species distributions (Woodward and Williams, 1987; Syfert et al., 2013). Points occurring outside the *A. adenophora*'s normal mean annual temperature and rainfall ranges, and were excluded from the analysis (Fig. A.1). Spatial data files were prepared for analysis in Maxent using Environmental Systems Research Institute's ArcGIS version 10.

2.3. Modeling the ecological niche of *A. adenophora*

We developed an ecological niche model of *A. adenophora* using Maxent 3.3.3k (Phillips et al., 2006; Phillips and Dudík, 2008; Phillips, 2008). We used Maxent for the reasons outlined in the Introduction. The ecological niche model was developed based on 10 random subsets of georeferenced occurrence points (70% of points used for calibration:30% for validation (Phillips et al., 2006)) of *A. adenophora* worldwide. We used linear and quadratic features whose outputs make ecological sense and are easier to interpret (Merow et al., 2013; Syfert et al., 2013). Since the choice of features has negligible effects on predictive performance, and sampling bias was accounted for, we considered simple feature types to be sufficient (Syfert et al., 2013). To

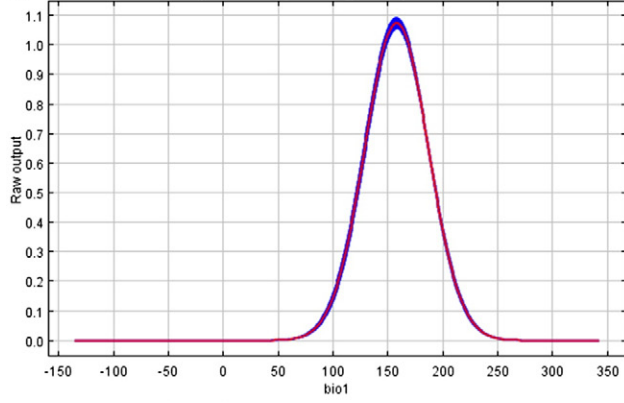
determine where the model was interpolating (estimating relative rate of occurrence (ROR) within a range of known presence points) or extrapolating (estimation of ROR outside the range presence data), multivariate environmental similarity surfaces (MESS maps *sensu* Elith et al., 2010) were produced. To determine model performance we computed the Lowest Presence Threshold (LPT) (Kumar and Stohlgren, 2009; Webber et al., 2011). We then converted the suitability indices in each grid cell to presence (suitable) and absence (unsuitable) using the LPT (Webber et al., 2011). We determined the model sensitivity, that is, the proportion of test locations accurately predicted. A model that is performing well should ideally encompass all test locations (Webber et al., 2011). To determine usefulness of the model, we computed prevalence (proportion of the study region estimated to be climatically suitable)—a small prevalence is better (Webber et al., 2011). Area under curve (AUC) was used to assess how well the model was able to discriminate between known presences and pseudo/assumed absences. The model output map was prepared using ArcGIS version 10.

2.4. Interpretation of the results

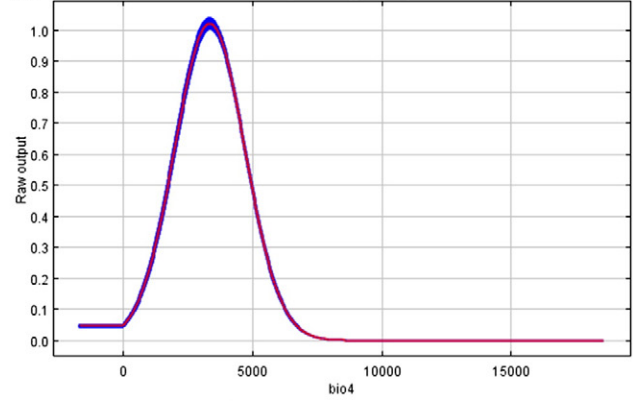
While we attempted to meet most of the assumptions of presence-only modeling, we took a cautious and modest approach in interpreting Maxent outputs following the advice of Yackulic et al. (2013). The raw output presented in the resulting map (Fig. 1) was interpreted as relative occurrence rate, not probability of occurrence (Elith and

Fig. 2. Mean response curves of 10 replicate Maxent runs (red) and the mean ± 1 standard deviation (blue). i. Graphs a–d show how the prediction changes as each variable varies and keeping all other environmental variables at an average sample value. ii. Graphs e–h show a Maxent model created using only the corresponding variable.

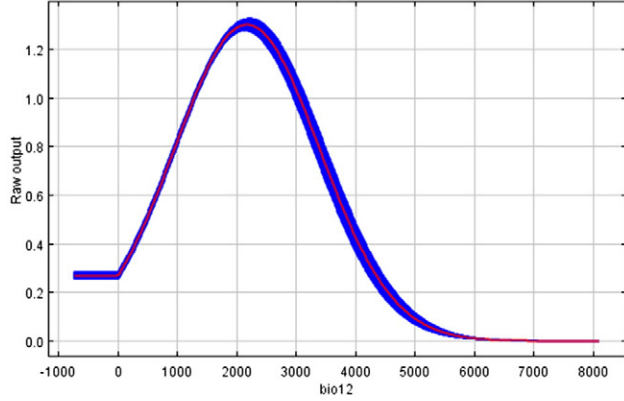
a. Response of *A. adenophora* to mean annual temperature



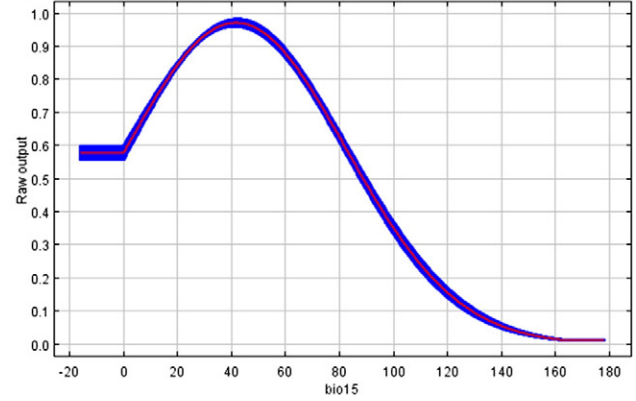
b. Response of *A. adenophora* to temperature seasonality



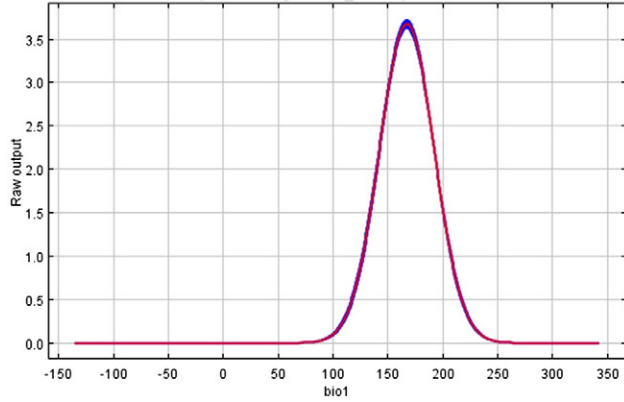
c. Response of *A. adenophora* to annual precipitation



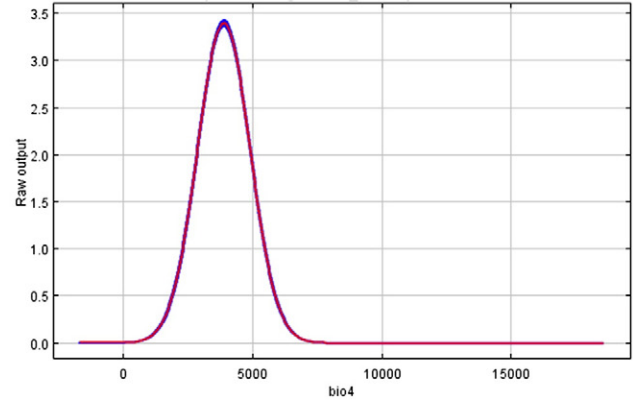
d. Response of *A. adenophora* to precipitation seasonality



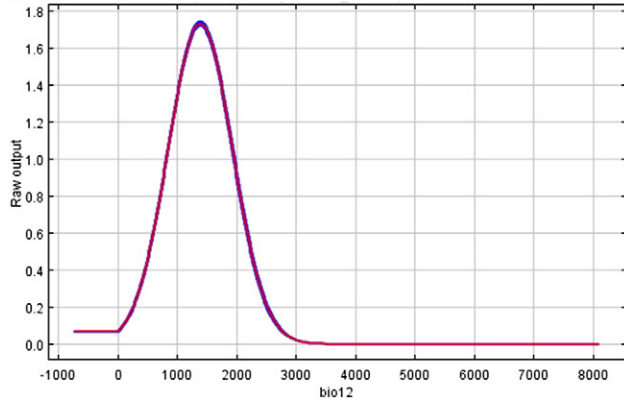
e. Response of *A. adenophora* to mean annual temperature only



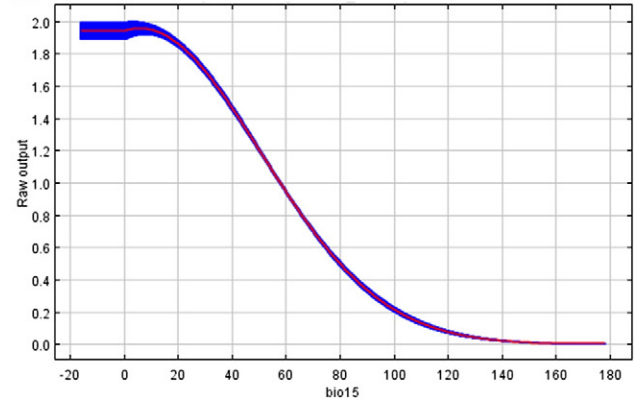
f. Response of *A. adenophora* to temperature seasonality only



g. Response of *A. adenophora* to annual precipitation only



h. Response of *A. adenophora* to precipitation seasonality only



Graham, 2009; Merow et al., 2013; Yackulic et al., 2013). We report here information on modeled relationships that is often unreported in many similar studies, e.g. number of covariates, relative importance of each covariate in the model, details about the “model that was fit” including response curves; number of features included in the model (giving an indication of model complexity), and number of data points. AUC measures the ability of predictions to discriminate between observed presence and absence (Elith and Graham, 2009), or in the case of presence-only modeling presence versus background (pseudo-absence) (Lobo et al., 2008; Yackulic et al., 2013). However it is considered to be potentially misleading (Lobo et al., 2008), therefore, it is given but not relied on for model accuracy. We mainly rely on sensitivity, prevalence and MESS and LPT for assessing model accuracy.

3. Results

3.1. Model results

The model projection tested against its training distribution records in its relevant training domain (i.e. the Köppen–Geiger derived background points) was found to be statistically significant using the exact binomial test ($p < 0.0001$). Clearly the model predicted some climatically suitable areas not currently occupied by the species (Fig. 1). Parts of the Eastern Cape, KwaZulu–Natal, Mpumalanga, and Gauteng emerged as the most suitable for *A. adenophora* occupancy. These regions coincided with *A. adenophora* occurrence records (Fig. 1). These are followed by the Western Cape and Limpopo provinces. Mean annual temperature (42.8%) and temperature seasonality (35.6%) make the biggest contributions to the Maxent model; and both exhibit a relatively narrower tolerance range for *A. adenophora* compared to precipitation (Fig. 2).

3.2. Model performance

The mean AUC for the 10 replicate models was 94% (Fig. A.3). MESS maps (Fig. A.4) showed that the output model was in interpolation mode (MESS +), except in the Sahara desert and the Arctic and sub-Arctic region. Our model predicted potentially suitable habitat for *A. adenophora* with good success rates, 83% at the LPT (0.0002), and was statistically significant ($p < 0.001$). Our model gave a sensitivity of 0.99, while the modeled prevalence was 0.21. According to the model, the Bioclim variable with the greatest influence on model prediction was mean annual temperature (Bio1), followed by temperature seasonality (Bio4) (Table A.1, Fig. A.5).

4. Discussion

Our ecological niche model predicted locations with suitable climatic conditions where *A. adenophora* can potentially establish. These predicted locations, including Mpumalanga, Gauteng, Kwazulu–Natal, Eastern Cape and Western Cape, are the sites where the species can naturalize, and not necessarily where it will be a problematic invader producing large dense infestations. The distribution of potential areas with high relative occurrence rate of *A. adenophora* follows areas with warm temperatures and high precipitation or generally wet micro-habitats. *A. adenophora* appears to prefer temperatures in the range of 10–25 °C; and low temperature and rainfall seasonality as shown by the response curves. This concurs with findings of studies in other parts of the world, especially the subtropics including southwest China and southeast Australia (see Sun et al., 2004, for a review).

If these areas are indeed climatically suitable, the absence of *A. adenophora* may be explained by factors not included in this model. A species may fail to colonize its fundamental or ecological niche because of human factors, biotic interactions (inter-specific competition, predation), and geographic barriers hindering dispersal (Peterson and Vieglais, 2001; Phillips et al., 2006). Interspecific species

interactions resulting from the presence of other invasive species such as *Lantana camara* L. (Baars and Naser, 1999) and *Chromolaena odorata* (L.) R.M. King & H. Rob. (Goodall and Zacharias, 2002) on the east coast may be limiting the spread of *A. adenophora* into these areas. A predicted potential distribution broader than the current distribution may be a result of the lack of niche conservatism (Peterson and Shaw, 2003; Peterson and Vieglais, 2001; Wiens et al., 2010) between native and invaded range for the species, that is, the ability of a species to broaden its ecological niche over time. Areas west and north of Lesotho are classified as having low to moderate risk of invasion by *A. adenophora*, and this may be a result of low annual temperatures. The derivation of a local model (South Africa) from a global dataset (Bioclim) may reduce accuracy (e.g. the prediction of areas beyond current occurrences). However, we consider such inaccuracies to be negligible since Maxent projected areas of climate suitability in interpolation (MESS +) space beyond the areas where *A. adenophora* is known to be present in South Africa. MESS + curbs extrapolation inaccuracies, a concern raised for modeling (Elith et al., 2010; Kriticos and Randall, 2001; Sutherst and Bourne, 2009).

A proper understanding of species invasions requires models that capture key determinants of the fundamental niche, and projections that are meaningful and reliable beyond the training regions (Webber et al., 2011). We therefore endeavored to ascertain that our model is sound by determining LPT, sensitivity and model prevalence, all of which confirmed that our model was sound. The fact that the LPT value prediction was significant shows that test points are predicted better than by a random prediction with the same fractional area predicted. We obtained good sensitivity for the model and this reduces the likelihood of underestimating invasive species risk (Webber et al., 2011). Our modeled prevalence was quite low. Webber et al. (2011) showed through the use of Fisher's exact one-tailed binomial and χ^2 tests that the smaller the prevalence, the lower the probability that all presence points would be included within the suitable area by chance alone. The model performance was thus good.

5. Implications for management

The results suggest that a large area is climatically suitable for *A. adenophora* to naturalize and potentially spread in South Africa. However, this species has not aggressively invaded all suitable areas, though it is becoming more widespread and is highly invasive in at least some parts of the country (Heystek et al., 2011). There is no room for complacency on the part of managers, as conditions may change to favor the spread of *A. adenophora* into areas that have been predicted as climatically suitable, especially changes in the disturbance regime (Richardson and van Wilgen, 2004), which our model did not consider. For the areas that are not currently occupied, but predicted suitable, pre-emptive measures may be necessary to prevent invasion (Trethowan et al., 2011).

Our study successfully addressed the main research question. It is clear that there is potential for *A. adenophora* to spread further than its current distribution. These findings can be applied in various ways including the identification of additional localities where *A. adenophora* may already exist, but has not yet been detected (Dudík et al., 2007); identification of localities where it is likely to spread to (Peterson and Shaw, 2003); and in combination with other information such as distribution of threatened ecosystems or biodiversity hotspots, identification of areas to prioritise for management. We suggest that a key intervention could be containment by preventing it from extending its range. However, a resulting key question is, “why has this species not spread rapidly in other parts of South Africa, despite a suitable climate?” Various factors that are operating locally, rather than internationally, and therefore not included in the model require investigation. Biotic factors identified as important to the plant's invasion elsewhere include changing soil microbe communities (Yu et al., 2005), and a changed energy-use strategy (Feng et al., 2011). Other possible biotic interactions that are playing a

role are interspecific competition by indigenous plants and impact of disturbance on this, as well as the effect of the introduced biological control agents, and this warrants further research.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.sajb.2014.09.001>.

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