

## Climate change may reduce the spread of non-native species

BEZENG S. BEZENG,<sup>1,†</sup> IGNACIO MORALES-CASTILLA,<sup>2,3,4</sup> MICHELLE VAN DER BANK,<sup>1</sup>  
KOWIYOU YESSOUFOU,<sup>5</sup> BARNABAS H. DARU,<sup>2</sup> AND T. JONATHAN DAVIES<sup>1,3</sup>

<sup>1</sup>Department of Botany and Plant Biotechnology, African Centre for DNA Barcoding, University of Johannesburg, APK Campus, PO Box 524, 2006 Johannesburg, South Africa

<sup>2</sup>Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138 USA

<sup>3</sup>McGill University, 1205 Avenue du Docteur-Penfield, Montreal, Quebec H3A 1B1 Canada

<sup>4</sup>Quebec Center for Biodiversity Science, McGill University, 1205 Avenue du Docteur-Penfield, Montreal, Quebec H3A 1B1 Canada

<sup>5</sup>Department of Geography, Environmental Management and Energy Studies, University of Johannesburg, APK Campus, 2006 Johannesburg, South Africa

**Citation:** Bezing, B. S., I. Morales-Castilla, M. van der Bank, K. Yessoufou, B. H. Daru, and T. J. Davies. 2017. Climate change may reduce the spread of non-native species. *Ecosphere* 8(3):e01694. 10.1002/ecs2.1694

**Abstract.** Invasive species are considered a major threat to ecosystem functioning and native biodiversity. Their negative impacts on ecosystems and the provisioning of ecosystem services have been widely documented. South Africa faces one of the most significant challenges from invasive species globally, and the South African government spent an estimated US \$100 million to mitigate impacts of non-native species between 1995 and 2000 alone. Here, we modeled the current climatic niche of 162 non-native trees and shrubs within South Africa and explored potential shifts in their distribution with projected climate change. Our results indicate that over half of these species will experience a decrease in their suitable climate over the next decades, although not uniformly so and ranges are predicted to expand into some regions. We also compared recent vs. historical introductions and showed similar patterns, indicating that possible violation of equilibrium assumptions in our distribution models likely does not strongly influence our findings. We suggest that climate change may therefore provide a window of opportunity for more effective invasive species control within South Africa, but that large range shifts are likely for many non-natives in the future, and new invasive threats might emerge.

**Key words:** non-native species; range shifts; species distribution models; trees and shrubs.

Received 23 August 2016; revised 20 December 2016; accepted 22 December 2016. Corresponding Editor: Debra P. C. Peters.

**Copyright:** © 2017 Bezing et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† E-mail: bezengsimmy@gmail.com

### INTRODUCTION

South Africa's woody flora is relatively small, with a total land area under forest cover of about 7% (Poynton 1979a, b, 2009), although the region is floristically diverse with approximately 8% of the world's vascular plants, and harbors three of the eight African plant biodiversity hotspots. However, a rapid increase in human population and associated rapid urbanization generated a large demand for timber, wood products, and other ecosystem services (e.g., soil stabilization)

that the slow rate of growth and wood production by South Africa's natural forest trees was unable to meet (Poynton 2009). To supply this demand, there was a large-scale introduction of fast-growing non-native tree species dating back to early European settlement. Many of the non-native tree species in South Africa today are a product of this ad hoc introduction program. This influx of non-native species has had profound ecological and economic impacts in South Africa and globally (Mack et al. 2000, Sala et al. 2000, Van Wilgen et al. 2001, Richardson and van

Wilgen 2004, Pimentel et al. 2005, Winter et al. 2009, Pyšek et al. 2010, Davies et al. 2011). For example, invasion of the fynbos biome, a global biodiversity hotspot, is estimated to have locally reduced native species richness by 45–67% (Higgins et al. 1999). In addition, the value of the over one million hectares of protected fynbos biome could be significantly reduced if invasive species remain unchecked, with an economic loss that might amount to several billion dollars over the next few decades (Higgins et al. 1999) through reduction in wild flower harvesting, ecotourism, and other natural services. To mitigate impacts of non-native species, between 1995 and 2000 the South African government spent an estimated US \$100 million on their eradication and management through the Working for Water (WfW) program (Van Wilgen et al. 2001).

Since the earliest introductions, dating to 1652, it is estimated that approximately 750 different non-native tree species have become established in South Africa, together with close to 8000 invasive, naturalized, and casual non-native shrubs, succulents, and herbaceous plants (Van Wilgen et al. 2001, Henderson 2006, see also a global review by Richardson and Rejmánek 2011). Managing and controlling the spread of non-natives outside their native range is an immense challenge (Van Wilgen et al. 2011), which is further compounded by potentially complex interactions between global climate change and species geographic distributions (Willis et al. 2008, 2010, Richardson et al. 2010). According to a recent report of the Intergovernmental Panel on Climate Change (IPCC), global mean temperatures are predicted to increase by up to 4°C toward the end of this century due to anthropogenic activities (IPCC 2014). Since the geographic pattern of plant distribution correlates primarily with climate, this warming is expected to have a major impact on future patterns of plant diversity through range expansions and contractions (Thomas et al. 2004, Thuiller et al. 2005, Loarie et al. 2008, Bradley 2009). Previous studies examining the effects of climate change on the potential distribution of invasive species have shown mixed patterns. Some have revealed a trend toward range expansion for invasive species with climate change (Bradley et al. 2009, Bellard et al. 2013), whereas others have shown a trend toward range reduction (Richardson et al.

2010, Wan et al. 2016). There is, therefore, no broad consensus as to how changing climatic conditions will impact species invasion, and further studies on how both non-native and native plant species will respond to new climatic regimes are needed (Sykes et al. 1996, Hamann and Wang 2006, Keith et al. 2009).

In recent years, researchers have developed tools that provide increasingly accurate models of species' abiotic niches. Species distribution models (SDMs) have been widely used to predict the potential impacts of climate change in South Africa and globally (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Richards et al. 2007, Richardson et al. 2010, see also a review by Elith and Leathwick 2009). By evaluating the correlations between current distribution data and climate, SDMs allow us to define the climate envelope of a species, and project forward under future climate change scenarios to identify geographic regions outside the current geographic range distribution that will fall within the species future climate envelope and, conversely, regions within the current range that will no longer be climatically suitable in the future (Peterson et al. 2002, Thomas et al. 2004, Thuiller et al. 2005, Elith and Leathwick 2009).

Here, we explore projected range shifts for 162 species of non-native woody trees and shrubs; these taxa represent 94 genera of gymnosperms and angiosperms spread over 36 families and 19 orders. Using >87,000 occurrence points and a variety of species distribution modeling algorithms, we modeled their potential distributions under current and future projected climate scenarios. Our analysis is the most extensive study to date on the distribution of woody non-native trees and shrubs in South Africa. Previous efforts to model species distributions for both non-natives and natives within South Africa have generally been taxonomically restricted, often focused on a single species, genera, or family (Bomhard et al. 2005, Richardson et al. 2010, Van Wilgen et al. 2011, Kaplan et al. 2012, Cabral et al. 2013). Our aim was to evaluate how non-native trees and shrubs are likely to respond to projected climate change, and to identify regions that might represent invasion hotspots in the future so as to help concentrate conservation efforts in order to reduce the high cost associated with their control and eradication.

## METHODS

### *Non-native species occurrence data*

A list of non-native species was obtained from the Southern African Plant Invaders Atlas (SAPIA) database. This catalogue contains the most up-to-date list of all naturalized/invasive non-native plant species in southern Africa, with information on the spatial distribution, abundance, habitat preference, and time of introduction for approximately 600 species (including herbs, grasses, climbers, aquatic plants, trees, and shrubs; Henderson 2001, but see also Henderson 2007). For the purpose of this study, we define non-invasive species as the combined set of naturalized and casual non-native plants from this list. Following Henderson (2007), we define invasive species as the subset of naturalized non-native plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants, and thus have the potential to spread over large areas. We include non-invasive species in our models because it is possible that, although they might not be problematic now, they might pose future invasive threats under climate change. Our study included a total of 162 non-native woody tree and shrub species for which detailed occurrence data could be readily obtained.

To maximize sampling of occurrence data, we combined the SAPIA database and PRECIS database of the National Herbarium in Pretoria (Germishuizen and Meyer 2003; which contains records for more than 900,000 specimens of native and non-native species distributed across 24,500 taxa from southern Africa). We additionally supplemented these data with sampling locations from the African Centre for DNA Barcoding, through the Toyota Enviro Outreach program (<http://toyotaoutreach2012.blogspot.co.za/>) and the national invasive DNA barcoding project of the WfW program. Point data were cleaned to remove records with doubtful or imprecise localities. The maximum number of point records was 5336, for the woolly nightshade (*Solanum mauritianum*), and the minimum was eight, for the stinging tree (*Wigandia urens*). Although there is a debate as to the accuracy of SDMs when occurrence records are sparse (Wisz et al. 2008), we included species with only few records to maximize taxonomic sampling. However, we conducted a sensitivity analysis to

explore robustness of our results by successively removing species with less than 20, 30, and 50 records.

### *Climatic data*

Current and projected climate data were extracted from the WorldClim database (<http://www.worldclim.org>; Hijmans et al. 2005), representing interpolated climate station records from 1950 to 2000, and projected future scenarios at 2.5-minute resolution. We included 19 climatic variables as potential predictors (Appendix S1). For future climate projections, we considered two general circulation models (GCMs) and three emission scenarios or representative concentration pathways (RCPs). We obtained spatially downscaled estimates of future climate for the year 2070 using the most up-to-date climate change projections from the IPCC Fifth Assessment Report. For each GCM (the Geophysical Fluid Dynamics Laboratory Climate Model version 3 [GFDL-CM3] and the Hadley Centre Global Environmental Model version 2), we analyzed the following RCPs: low RCP = 2.6; medium RCP = 4.5; and high RCP = 8.5. Climatic projections predict temperature changes of 1.1–4.5°C and precipitation changes of 2.1–4.6% by the end of the century (Baek et al. 2013).

### *Determination of suitable climate*

We applied two classes of SDMs that use either presence–background data or presence–absence data to establish current and future climate suitability of all 162 woody non-native trees and shrubs in our data set. For presence–background data, we used MaxEnt version 3.3.3 (Phillips et al. 2006) as it outperforms similar methods and has been shown to provide accurate predictions even when only few occurrence points are available (Elith et al. 2006, Wisz et al. 2008). For each MaxEnt model, we ran 15 sub-sampling replicates to generate an average model to account for variability among runs, and 5000 iterations per replicate per species, which was sufficient for model convergence. For presence–absence data, we constructed ensemble forecasts (Araújo and New 2007) from three alternative SDM algorithms: generalized linear models (GLMs; Guisan et al. 2002), random forests (RFs; Breiman 2001), and the gradient boosting machine (GBM; Friedman and Tibshirani 2000). Since we lack actual absence

data, we used background data, which characterize the environmental conditions of the study area, as pseudo-absences (Phillips et al. 2009). For each algorithm, we sampled pseudo-absences randomly across the study area assuming 1.5 times the number of presence points for each species and applied the same threshold approach for predicting species presence or absence to both current and future climate projections. Higher number of pseudo-absences, especially for machine-learning algorithms, should be avoided as this may negatively affect model accuracy (Barbetti-Massin et al. 2012). In all models, we accounted for collinearity of climate predictors by removing predictors with correlations  $>\pm 0.8$  with either mean annual temperature or mean annual precipitation. We assigned 25% of our occurrence data for testing and the remaining 75% for model training. Duplicate occurrence records were excluded to reduce model overfitting.

Model outputs followed a logistic distribution, ranging from 0 (climatically unsuitable areas) to 1 (climatically suitable areas). As yet, no consensus has been reached on choosing an appropriate threshold for transforming the modeled probability of occurrence into predictions of species presence or absence. Since threshold selection might affect results (Liu et al. 2005), we followed a two-fold procedure to minimize such impacts. For the MaxEnt model, we selected a 10-percentile training presence threshold to produce prediction probability maps (Ficetola et al. 2007, Phillips and Dudik 2008). To obtain ensemble forecast from the GLM-RF-GBM SDM, predictions were scaled to range from 0 to 1 and averaged weighted by the square of their AUC (Area Under the Curve) values, which gives more weight in the combined prediction to the algorithm that performs better (Ranjitkar et al. 2014, Breiner et al. 2015); predictions with AUC values below 0.5 (i.e., random expectation) were given zero weight. Averaged predictions were then transformed into binary maps by applying the threshold that maximizes the sum of the true-positive rate and the true-negative rate, thus minimizing model error for each species model (Manel et al. 2001). The thresholds obtained by cross-validation of each algorithm were also averaged weighted by the square of their AUC values above 0.5, and the resulting average species-specific threshold was applied.

#### *Comparison of current vs. future climates*

For both the MaxEnt outputs and GLM-RF-GBM ensemble forecasts, we quantified the difference in geographic extent of projected distributions between current and future climate scenarios. Negative values indicate a net reduction in climatically suitable areas with climate change, whereas positive values indicate a net expansion of climatically suitable areas with climate change.

Because recently introduced non-native species might not have had long enough residence time to expand their non-native distribution and reach equilibrium with the environment, it is possible that SDMs might misspecify the climate niche of these species. We therefore explored model sensitivity by evaluating the relationship between change in area of the predicted climate envelope and time of earliest dates of introduction across all GCMs and SDM methods. We used a non-parametric Mann-Whitney *U* test to compare pre- and post-1900 introductions, and a regression analysis of change in climate envelope area vs. date of introduction. This latter timeframe (post-1900) coincides with the formation of the Union of South Africa, and represents a period of rapid globalization. We hypothesized that if more recently introduced species have not had enough time to reach their available climate bounds, we might see a significant difference in projected range shifts between the pre- and post-1900 introduction events. Lastly, we explored potential differences in the important climate variables driving range shifts for pre- and post-1900 introductions by running correlations of per-cell change in predicted richness against change in each of the environmental variables in turn (i.e., whether a large change in temperature, for example, predicted a similar increase in the richness of both pre- and post-1900 introductions). We suggest that significant differences in the richness correlations with climate predictors between historical vs recent introductions could indicate either that models for recent introductions were unstable or that there was some qualitative difference in the ecology of recent vs. historical introductions. Cells that fell outside 1.5 times the interquartile range of environmental shifts were excluded from the correlation analysis.

## RESULTS

Under current climatic conditions, hotspots of suitable climates for non-native and invading trees and shrubs are centered in the Western Cape, Eastern Cape, Kwazulu-Natal, Mpumalanga, Limpopo, Gauteng, and part of the North West provinces (Fig. 1A; areas in red). However, our results from future projections across all scenarios suggest that over half of the species in our analyses may experience a decrease in their suitable climate space (mean percent of species showing a decrease across all SDMs, GCMs, and emissions scenarios = 63.3%), with the MaxEnt-GFDL-CM3-8.5 showing the highest percentage of species decreasing in extent (80%; Fig. 2). Averaged across all GCMs, the two species predicted to show the greatest contraction in potential range area at the country level were the hairy hakea (*Hakea gibbosa*) and the screw-pod wattle (*Acacia implexa*) both native to Australia, with the former predicted to show an average decrease of  $\sim 12 \times 10^3 \text{ km}^2$  and the latter an average decrease of  $\sim 27 \times 10^3 \text{ km}^2$  (Appendix S2).

Results were qualitatively similar across all GCMs, emission scenarios, and species distribution modeling algorithms (Fig. 2). The general trend for contraction of suitable climate was additionally robust to the removal of species with fewer occurrence points: Excluding species with less than 20, 30, and 50 occurrence points had little impact on overall trends for contraction in extent of suitable climate across species (Appendix S3).

By mapping the difference in predicted species distributions between present and future climate scenarios, we identify a number of regions where the threat of invasion from current non-native species might recede, including the provinces of Western Cape, Eastern Cape, Gauteng, KwaZulu-Natal, Mpumalanga, and Limpopo (Fig. 1B, areas in blue; see Appendix S4 for equivalent figure assuming RCP 8.5).

Although we predict that a majority of non-natives will experience a contraction in areas of suitable climate, averaged across all scenarios and SDMs 36.7% of species are still predicted to experience a range expansion. As such, we predict further spread of these species into some areas (Fig. 1B; areas in red) despite what may be a general decline in non-native range extent. Averaging

across all scenarios, the two species with the most significant expansion in potential range area were the red ironbark (*Eucalyptus sideroxylon*), native to Australia, and the Chilean mesquite (*Prosopis chilensis*) from South America, with predicted range expansions of  $\sim 347 \times 10^3$  and  $\sim 460 \times 10^3 \text{ km}^2$ , respectively (see Appendix S2). The provinces of Mpumalanga and Limpopo may be particularly vulnerable to future spread of non-natives with the KwaZulu-Natal, Free State, and North West provinces showing a mixed pattern of range expansion and contraction (Fig. 1B).

### Range shifts and dates of introduction

Our estimates of shifts in suitable climate might be less reliable for more recently introduced species if these taxa have not had sufficient time to occupy all potential climatically suitable regions (i.e., species have not obtained climatic equilibrium). Species distribution models for these species might underestimate their true climate niche. We therefore compared trends between more recently introduced taxa (post-1900) and species that were introduced prior to 1900. From the list of species in our data set, 72 species had records indicating introduction prior to 1900, and 43 species were introduced post-1900, whereas well-established dates of introduction for the remaining 47 species could not accurately be determined (Appendix S5). We found no statistically significant difference in predicted change in areas of suitable climate between pre- and post-1900 introduction events across all GCMs and emission scenarios ( $P > 0.05$ ). However, we observed a stronger signal of geographic range contraction for the Free State province in the post-1900 introduction (Fig. 3A,B). Further, there is a significant negative correlation between time since introduction and change in range size (slope =  $-1.68$ ,  $P = 0.02$ ; Appendix S6), such that more recently introduced species are predicted to show a greater decrease in geographic extent with climate change, although the relationship is weak ( $r^2 = 0.04$ ).

Last, to explore whether the environmental drivers of range shifts differed between post- and pre-1900 introduction events, we examined correlations between changes in predicted richness against changes in each of the environmental predictor variables included in our SDMs. We found that similar temperature-based and precipitation-based bioclimatic variables (i.e., the

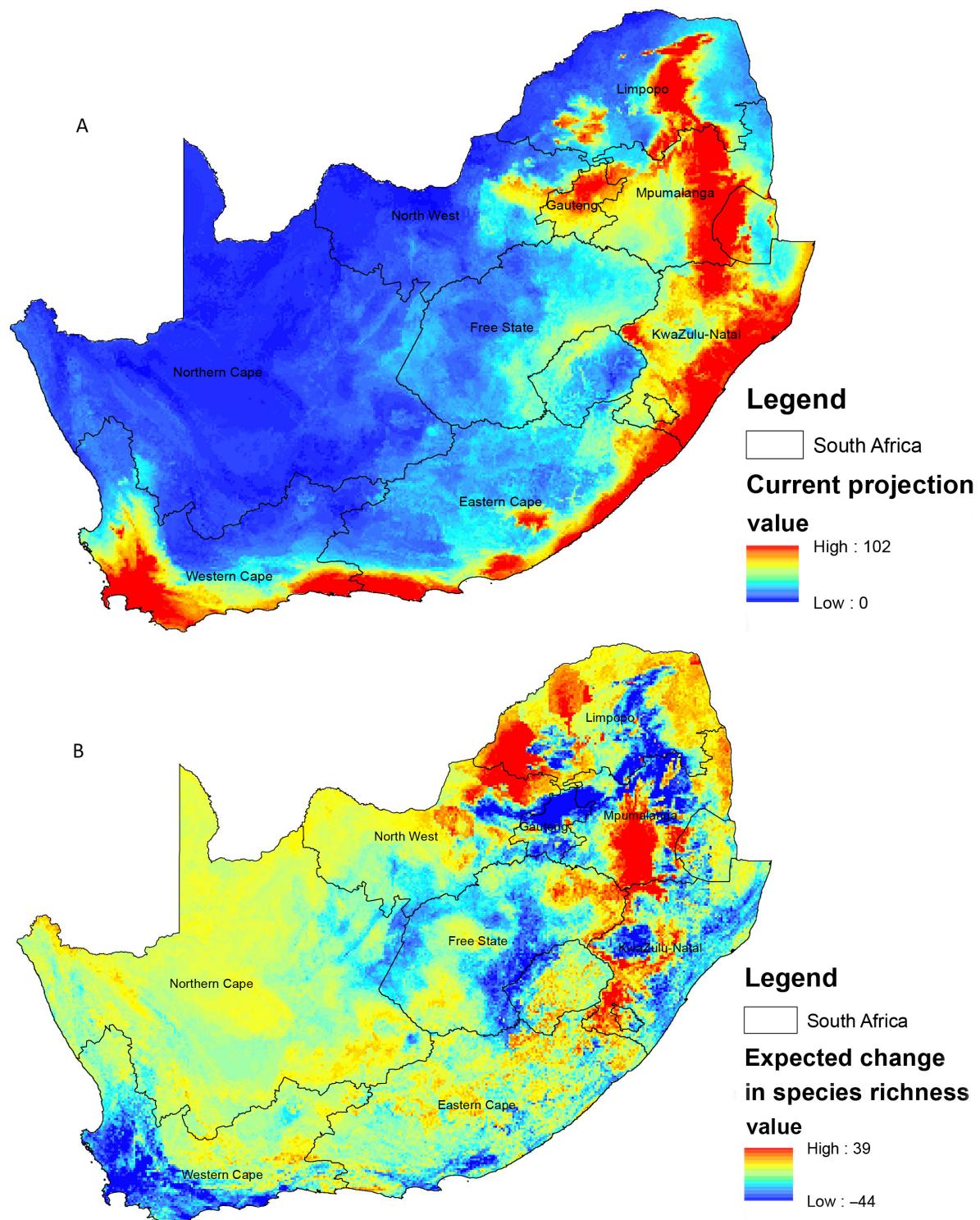


Fig. 1. (A) Climate suitability map derived from stacking individual species distributions. Red colors indicate areas that are potentially suitable for a higher number of species. (B) Change in potential species richness between current and projected climate for the year 2070 for all 162 non-native woody taxa. Red areas (positive values) highlight regions that may be particularly vulnerable to spread of non-native species in the future; blue areas (negative values) highlight regions where the threat from current invasion might recede. Both panels show results from ensemble forecasts using current climate and the future climate projection for 2070 under the Geophysical Fluid Dynamics Laboratory Climate Model version 3\_2.6 climate scenario.

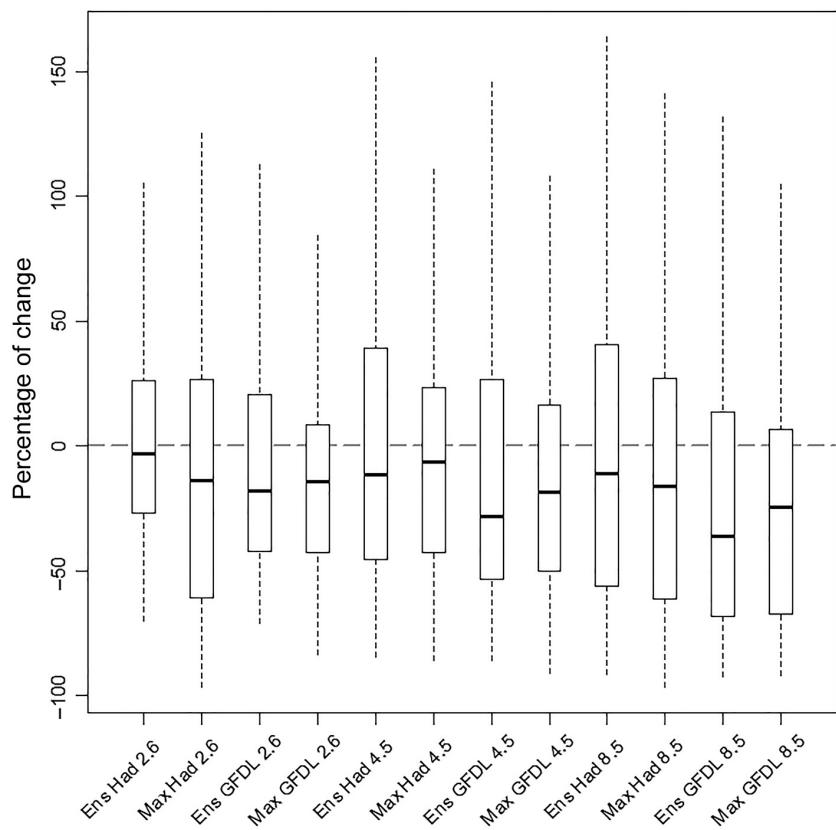


Fig. 2. Percent change in extent of suitable climate space from species distribution models fitted to current climate and each of the climate change general circulation models (GCMs) and emission scenarios. Each boxplot represents the variation in the net effects of climate change across all 162 species modeled according to the following combinations of species distribution model algorithms, GCMs, and representative concentration pathway: Ensemble Forecast-HadGEM2-AO\_2.6 Ens Had 2.6, MaxEnt-HadGEM2-AO\_2.6 Max Had 2.6, Ensemble Forecast-GFDL-CM3\_2.6 Ens GFDL 2.6, MaxEnt-GFDL-CM3\_2.6 Max GFDL 2.6, Ensemble Forecast-HadGEM2-AO\_4.5 Ens Had 4.5, MaxEnt-HadGEM2-AO\_4.5 Max Had 4.5, Ensemble Forecast-GFDL-CM3\_4.5 Ens GFDL 4.5, MaxEnt-GFDL-CM3\_4.5 Max GFDL 4.5, Ensemble Forecast-HadGEM2-AO\_8.5 Ens Had 8.5, MaxEnt-HadGEM2-AO\_8.5 Max Had 8.5, Ensemble Forecast-GFDL-CM3\_8.5 Ens GFDL 8.5, and MaxEnt-GFDL-CM3\_8.5 Max GFDL 8.5. GFDL-CM3, Geophysical Fluid Dynamics Laboratory Climate Model version 3; HadGEM2-AO, Hadley Centre Global Environmental Model version 2.

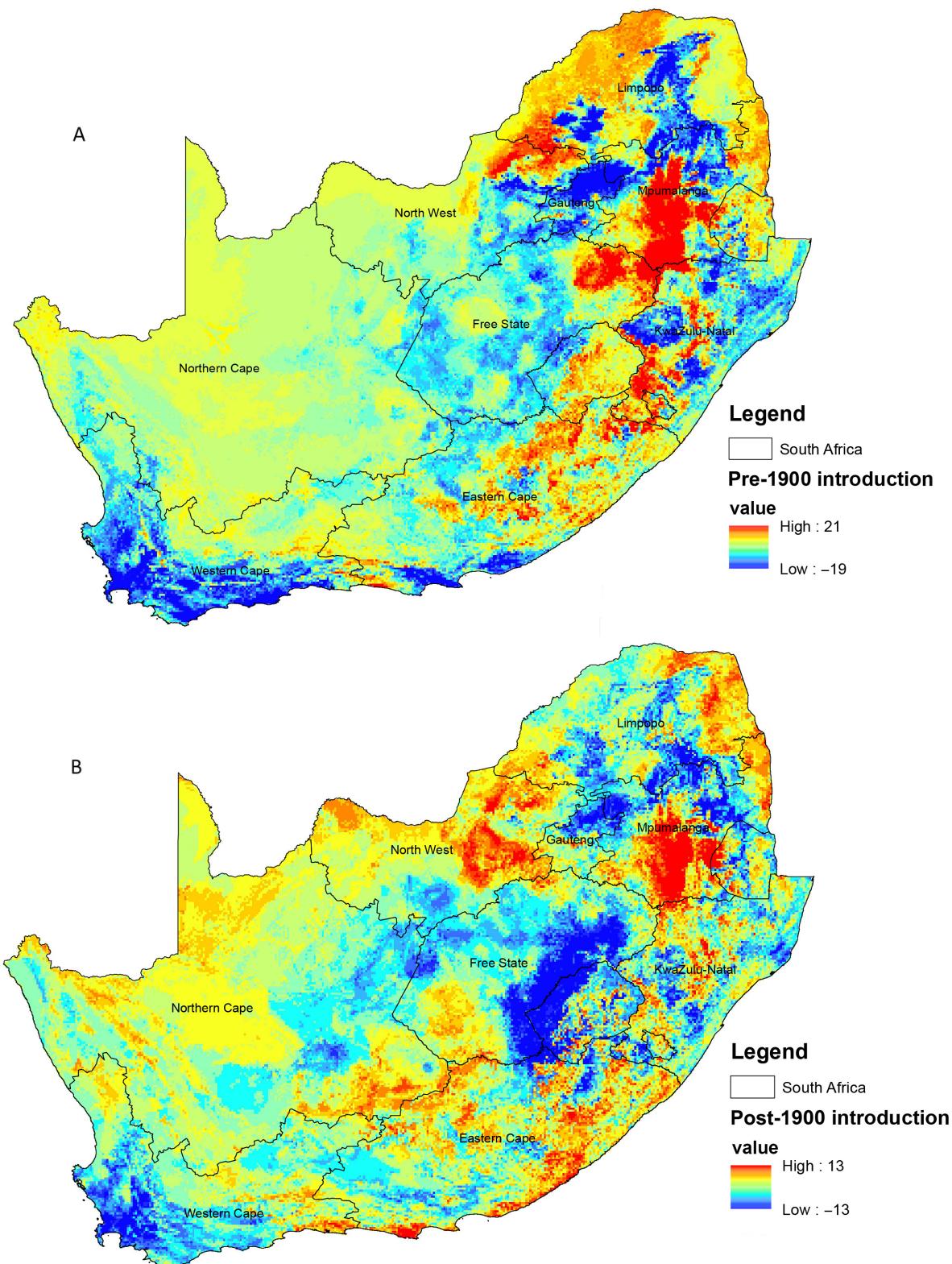


Fig. 3. Predicted shift in range distributions under projected climate change, highlighting regions of range expansion (red) and contraction (blue) for non-native species introduced before 1900 (A) and non-native species introduced after 1900 (B). Values calculated as described for Fig. 1, and based on results from ensemble forecasts using current climate and the future climate projection for 2070 under the Geophysical Fluid Dynamics Laboratory Climate Model version 3 representative concentration pathway = 2.6 climate scenario.

19 WorldClim bioclimatic variables excluding temperature seasonality, temperature annual range, and precipitation of warmest quarter) were important in explaining range shifts for both taxon sets across GCMs (Appendix S7). We also found the correlation strengths between percent change in richness and the change in temperature-based and precipitation-based bioclimatic variables to be highly correlated between pre- and post-1900 introductions (e.g.,  $r^2 = 0.82$  from the correlation of climate predictor correlation strengths from the ensemble forecast SDM under the GFDL-CM3\_2.6 climate projection scenario for pre- and post-1900 introductions); thus, equivalent shifts in richness were predicted for recent and historical (pre-1900) introductions for a given change in environment.

## DISCUSSION

There is increasing evidence that anthropogenic activities are driving climate change and that rates of change are likely to increase in the future (Lenton et al. 2008, IPCC 2014). Many species are predicted to shift their current distributions to track their climate niche, for example, moving to higher latitudes or upward in elevation (Lenoir et al. 2008, Loarie et al. 2009). Several studies have attempted to model the future potential distribution of non-native and invasive species in South Africa and globally, and many have shown projected increases in their range sizes with climate change (Walther et al. 2009, Trethowan et al. 2011, Bradley et al. 2012). In one recent example, Bellard et al. (2013) modeled the potential future distribution for 100 of the world's most invasive non-native species and predicted that a majority of these species would expand their ranges northward. However, other studies have projected range contraction for some species (Richardson et al. 2010, Wan et al. 2016).

Here, we used SDMs and future climate projections, employing different GCMs and future emission scenarios, to explore the potential shift

in the distribution of non-native trees and shrubs in South Africa. We showed that, on average, the geographic extent of suitable climate space for a majority of these species is predicted to contract in the future. Results were generally consistent across alternative algorithms, emission scenarios, and GCMs.

Projecting future distributions, we identified some regions where threats from non-native species might lessen including the provinces of the Western Cape, Eastern Cape, Gauteng, KwaZulu-Natal, Mpumalanga, and Limpopo. We found similar trends of decrease in climate suitability after removing species with few occurrence points, for which range projections might be less accurate. However, species' responses are idiosyncratic, and models still predict the potential for an increased spread of some species with climate change. In addition, some non-native species might not yet occupy all currently suitable climate space available to them because they may not have reached climatic equilibrium. Hence, these species may continue to spread in their geographic distribution even though the total area of suitable climate might remain unchanged or even decrease (García-Valdés et al. 2013).

Under current climatic conditions, potential hotspots for non-native trees and shrubs in South Africa include the Western Cape, Eastern Cape, KwaZulu-Natal, Mpumalanga, Gauteng, Limpopo, and part of the North West provinces. These provinces have previously been identified as major source pools for many non-natives because of their high rainfall, high urban development, farming, and silvicultural practices (Schulze 1997, Henderson 2006, 2007, Poynton 2009). Under projected climate change, several additional geographic regions, for example, Mpumalanga and Limpopo provinces, may be particularly vulnerable to range expansion of non-native species in the future. These provinces represent high elevation or topographically variable regions, suggesting that climate change might drive many species to move into areas of high elevation (Rebelo and

Siegfried 1992, Richardson et al. 1996, Bomhard et al. 2005, Loarie et al. 2009, Bellard et al. 2013).

While species distribution modeling provides a powerful tool for exploring effects of climate change on species invasion, several challenges remain as to its implementation.

First, because invasion is a dynamic process (Dostál et al. 2013), it is possible that SDMs generated from the non-native range mischaracterize the true climatic envelope (or fundamental climatic niche) for some species, especially for recent introductions, which may not yet have had sufficient time to reach equilibrium with their environments (Guisan and Zimmermann 2000, Araújo and Pearson 2005, Thuiller et al. 2005, Václavík and Meentemeyer 2009, 2012). One alternative approach would be to generate SDMs trained with data from the native range (Mau-Crimmins et al. 2006, Broennimann and Guisan 2008, Beaumont et al. 2009, Trethowan et al. 2011, Kaplan et al. 2012, O'Donnell et al. 2012). We lacked detailed distribution data on the native range for most species considered here; however, previous studies have shown that models trained on native range data can be a poor estimate of the fundamental climate niche of a species, as illustrated by the fact that many non-natives expand beyond the climate envelope realized in their native distribution (Rödder and Lötters 2009). Therefore, the inclusion of native range data might reduce, rather than enhance, model accuracy (see discussion in Rödder and Lötters 2009 and references therein), and we found mixed results for a subset of taxa for which we had detailed data on the native distribution (results not shown).

We evaluated the sensitivity of our results by comparing pre- and post-1900 introductions. If more recently introduced species have not yet had sufficient time to reach the boundaries of their climate niche, then we might expect differences in the predictions of range shifts between early and recent introductions. We found that the likelihood to expand or contract in range was similar between pre- and post-1900 introductions and that similar climate variables drive range shifts in both taxon sets, which suggests that the violation of the equilibrium assumption does not strongly influence our results.

Second, dispersal limitations and biotic interactions (e.g., inter- and intra-specific competition, predation, disease, mutualisms) are known to be

important in the spread of invasive species (Meentemeyer et al. 2008), and also likely influence the fit of SDMs (Schelderman and van Zonnenveld 2010). Unfortunately, we lack information to incorporate such interactions into our models, which would additionally require modeling how those interactions vary through time with climate change. While adding such complexities into our SDM predictions is not currently feasible, it represents an exciting avenue for future research on plant invasions.

Third, SDMs must also account for the variability in outcomes produced by different modeling techniques and data sources (i.e., different GCMs and RCPs; Araújo and Peterson 2012). We considered four SDM algorithms, two GCMs, and three different emission scenarios, and show results to be highly consistent (see also Loarie et al. 2008, O'Donnell et al. 2012, Bellard et al. 2013). Nevertheless, we emphasize that SDMs themselves provide only a probabilistic framework for modeling potential species distributions, and these need to be validated using empirical data as multiple factors including modes of dispersal, propagule pressure, species interactions, and geographic barriers will all influence the realized distribution of a species (Schelderman and van Zonnenveld 2010).

Despite limitations of current methods and data, our results match to some earlier studies on native species in this region. For example, a majority of species in the South African Proteaceae are predicted to experience a range contraction with climate change, and some species might even experience a complete loss of bioclimatic suitable space (Midgley et al. 2002, Bomhard et al. 2005, Cabral et al. 2013). In a study on the potential distribution of the invasive Peruvian pepper tree (*Schinus molle*), Richardson et al. (2010) also showed that the future range of this species will likely contract (see also results by Wan et al. 2016). Here, we have shown that this trend of range contraction with projected climate change might be a more general feature for non-native trees and shrubs in South Africa.

#### *Implications for non-native species management under climate change*

The rapid urbanization of South Africa has generated a demand for goods and services that the native flora is unable to meet. This gap has led to

the introduction of fast-growing non-native trees to supply the needs of the growing human population. Many of these introduced species have become invasive and pose a threat to native biodiversity. However, we have shown here that the potential area of suitable climate for many of these species may reduce with projected climate change. Assuming that geographic extent correlates with impact, our results may suggest that the impact of non-native species might be lessened in the future. Nonetheless, some regions are predicted to become more suitable for non-native species, including the Mpumalanga, KwaZulu-Natal, Free State, North West, and Limpopo provinces. Additionally, some species are still projected to show potential increases in their geographic ranges (e.g., *Eucalyptus sideroxylon* and *Prosopis chilensis*, the two species with the greatest potential for range expansion). These results are consistent with previous studies, and in some cases, management initiatives are already in place for their control (Zachariades et al. 2011).

We suggest that the regions and species identified above should be the focus for management interventions in South Africa. Further, newly introduced species that have yet to establish might pose novel threats. It is essential, therefore, that current efforts to control the introduction and eradication of currently invading species, for example, through program such as the early detection and rapid response initiative of the South African National Biodiversity Institute, be continued. Importantly, the contraction of suitable climate for many non-native species might also provide new opportunities for habitat restoration through assisted recolonization of native species that once occupied these regions (Bradley et al. 2009). These opportunities should be seized upon as they represent a rare opening in the ongoing battle against species invasions.

## ACKNOWLEDGMENTS

We wish to thank Lesley Henderson of the Agricultural Research Council—Plant Protection Research Institute—and Les Powrie of South African National Biodiversity Institute for sharing vital information, the International Development Research Centre (IDRC), Canada, and the University of Johannesburg Global Excellence and Stature (GES) Postgraduate Scholarship for funding. I.M-C acknowledges funding from the

Fonds de Recherches du Québec—Nature et Technologies (FQRNT) program. Lastly, we would like to thank two anonymous reviewers for comments on an earlier draft of this manuscript.

## LITERATURE CITED

- Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. *Trends in Ecology and Evolution* 22:42–47.
- Araújo, M. B., and R. G. Pearson. 2005. Equilibrium of species' distributions with climate. *Ecography* 28: 693–695.
- Araújo, M. B., and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93:1527–1539.
- Baek, H. J., et al. 2013. Climate change in the 21st century simulated by HadGEM2-AO under representative concentration pathways. *Asia-Pacific Journal of Atmospheric Sciences* 49:603–618.
- Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution* 3:327–338.
- Beaumont, L. J., R. V. Gallagher, W. Thuiller, P. O. Downey, M. R. Leishman, and L. Hughes. 2009. Developing climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions* 15:409–420.
- Bellard, C., W. Thuiller, B. Leroy, P. Genovesi, M. Bakkenes, and F. Courchamp. 2013. Will climate change promote future invasions? *Global Change Biology* 19:3740–3748.
- Bomhard, B., et al. 2005. Potential impacts of future land use and climate change on the Red List status of the Proteaceae in the Cape Floristic Region, South Africa. *Global Change Biology* 11: 1452–1468.
- Bradley, B. A. 2009. Regional analysis of the impacts of climate change on cheat grass invasion shows potential risk and opportunity. *Global Change Biology* 15:96–208.
- Bradley, B. A., M. Oppenheimer, and D. S. Wilcove. 2009. Climate change and plant invasions: Restoration opportunities ahead? *Global Change Biology* 15:1511–1521.
- Bradley, B. A., et al. 2012. Global change, global trade, and the next wave of plant invasions. *Frontiers in Ecology and the Environment* 10:20–28.
- Breiman, L. 2001. Random forests. *Machine Learning* 45:5–32.
- Breiner, F. T., A. Guisan, A. Bergamini, and M. P. Nobis. 2015. Overcoming limitations of modelling rare

- species by using ensembles of small models. *Methods in Ecology and Evolution* 6:1210–1218.
- Broennimann, O., and A. Guisan. 2008. Predicting current and future biological invasions: both native and invaded ranges matter. *Biology Letters* 4:585–589.
- Cabral, J. S., et al. 2013. Impacts of past habitat loss and future climate change on the range dynamics of South African Proteaceae. *Diversity and Distributions* 19:363–376.
- Davies, T. J., et al. 2011. Extinction risk and diversification are linked in a plant biodiversity hotspot. *Plos Biology* 9:e1000620.
- Dostál, P., J. Müllerová, P. Pyšek, P. Pergl, and T. Klinarová. 2013. The impact of an invasive plant changes over time. *Ecology Letters* 16:1277–1284.
- Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics* 40:677–697.
- Elith, J., et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Ficetola, G. F., W. Thuiller, and C. Miaud. 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. *Diversity and Distributions* 13:476–485.
- Friedman, J. H., and R. T. Tibshirani. 2000. Additive logistic regression: a statistical view of boosting. *Annals of Statistics* 28:337–374.
- García-Valdés, R., M. A. Zavala, M. B. Araujo, and D. W. Purves. 2013. Chasing a moving target: projecting climate change-induced shifts in non-equilibrium tree species distributions. *Journal of Ecology* 101:441–453.
- Germishuizen, G., and N. L. Meyer. 2003. Plants of southern Africa: an annotated checklist. *Strelitzia* 14:1–1231.
- Guisan, A., T. C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157:89–100.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Hamann, A., and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* 87:2773–2786.
- Henderson, L. 2001. Alien weeds and invasive plants: a complete guide to declared weeds and invaders in South Africa. PPRI Handbook No. 12. ARCPRI, Pretoria, South Africa.
- Henderson, L. 2006. Comparisons of invasive plants in southern Africa originating from southern temperate, northern temperate and tropical regions. *Bothalia* 36:201–222.
- Henderson, L. 2007. Invasive, naturalized and casual alien plants in southern Africa: a summary based on the Southern African Plant Invaders Atlas SAPIA. *Bothalia* 37:215–248.
- Higgins, S. I., D. M. Richardson, R. M. Cowling, and T. H. Trinder-Smith. 1999. Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conservation Biology* 13: 303–313.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:965–1978.
- Intergovernmental Panel on Climate Change IPCC. 2014. Summary for policymakers. Pages 1–32 in C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, and L. L. White, editors. *Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, USA.
- Kaplan, H., H. W. F. Van Zyl, J. J. Le Roux, D. M. Richardson, and J. R. U. Wilson. 2012. Distribution and management of *Acacia implexa* Benth. in South Africa: A suitable target for eradication? *South African Journal of Botany* 83:23–35.
- Keith, S. A., A. C. Newton, R. J. H. Herbert, M. D. Morecroft, and C. E. Bealey. 2009. Non-analogous community formation in response to climate change. *Journal of Nature Conservation* 17:228–235.
- Lenoir, J., J. C. Gegout, P. A. Marquet, P. De Ruffray, and H. Brisson. 2008. A Significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771.
- Lenton, T. M., et al. 2008. Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Science USA* 105:1786–1793.
- Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28: 385–393.
- Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. *Nature* 462:1052–1057.
- Loarie, S. R., et al. 2008. Climate change and the future of California's endemic flora. *PLoS ONE* 3:e2502.

- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasion: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38:921–931.
- Mau-Crimmins, T. M., H. R. Schussman, and E. L. Geiger. 2006. Can the invaded range of a species be predicted sufficiently using only native-range data? Lehmann lovegrass *Eragrostis lehmanniana* in the southwestern United States. *Ecological Modelling* 193:736–746.
- Meentemeyer, R. K., B. Anacker, W. Mark, and D. M. Rizzo. 2008. Early detection of emerging forest disease using dispersal estimation and ecological niche modeling. *Ecological Applications* 18: 377–390.
- Midgley, G. F., L. Hannah, D. Millar, M. Rutherford, and L. W. Powrie. 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography* 11:445–451.
- O'Donnell, J., R. V. Gallagher, P. D. Wilson, P. O. Downey, L. Hughes, and M. R. Leishman. 2012. Invasion hotspots for non-native plants in Australia under current and future climates. *Global Change Biology* 18:617–629.
- Peterson, A. T., et al. 2002. Future projections for Mexican faunas under global climate change scenarios. *Nature* 416:626–629.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modelling of species geographic distributions. *Ecological Modelling* 190: 231–259.
- Phillips, S. J., and M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161–175.
- Phillips, S. J., M. Dudík, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19:181–197.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien invasive species in the United States. *Ecological Economics* 52:273–288.
- Poynton, R. J. 1979a. Tree planting in Southern Africa. Vol 1: the Pines. Department of Forestry, Pretoria, Republic of South Africa.
- Poynton, R. J. 1979b. Tree planting in Southern Africa. Vol. 2: the Eucalypts. Department of Forestry, Pretoria, Republic of South Africa.
- Poynton, R. J. 2009. Tree planting in Southern Africa. Volume 3: other genera. Department of Agriculture, Forestry and Fisheries, Pretoria, South Africa.
- Pyšek, P., et al. 2010. Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Science USA* 107:12157–12162.
- Ranjitkar, S., J. Xu, K. K. Shrestha, and R. Kindt. 2014. Ensemble forecast of climate suitability for the Trans-Himalayan Nyctaginaceae species. *Ecological Modelling* 282:18–24.
- Rebelo, A. G., and W. R. Siegfried. 1992. Where should nature reserves be located in the Cape Floristic Region, South Africa? Models or the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity. *Conservation Biology* 6:243–252.
- Richards, C. L., B. C. Carstens, and L. L. Knowles. 2007. Distribution modelling and statistical phylogeography: an integrative framework for generating and testing alternative biogeographical hypotheses. *Journal of Biogeography* 34:1833–1845.
- Richardson, D. M., and M. Rejmánek. 2011. Trees and shrubs as invasive alien species—a global review. *Diversity and Distributions* 17:788–809.
- Richardson, D. M., and B. W. van Wilgen. 2004. Invasive alien plants in South Africa: How well do we understand the ecological impacts? *South African Journal of Science* 100:45–52.
- Richardson, D. M., B. W. Van Wilgen, S. I. Higgins, T. H. Trinder-Smith, R. M. Cowling, and D. H. McKell. 1996. Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. *Biodiversity Conservation* 5:607–647.
- Richardson, D. M., et al. 2010. Accommodating scenarios of climate change and management in modelling the distribution of the invasive tree *Schinus molle* in South Africa. *Ecography* 33: 1049–1061.
- Rödder, D., and S. Lötzter. 2009. Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko *Hemidactylus turcicus*. *Global Ecology and Biogeography* 18:674–687.
- Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Scheldeman, X., and van Zonneveld M. 2010. Training manual on spatial analysis of plant diversity and distribution. Pages 139–152. Biodiversity International, Rome, Italy.
- Schulze, R. E. 1997. Climate. Pages 21–24 in R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. *Vegetation of southern Africa*. Cambridge University Press, Cambridge, UK.

- Sykes, M. T., I. C. Prentice, and W. Cramer. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climate. *Journal of Biogeography* 23:203–233.
- Thomas, C. D., A. Cameron, and R. E. Green. 2004. Extinction risk from climate change. *Nature* 427: 145–148.
- Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Science USA* 102:8245–8250.
- Trethowan, P. D., M. P. Robertson, and A. J. McConnachie. 2011. Ecological niche modeling of an invasive alien plant and its potential biological control agents. *South African Journal of Botany* 77:137–146.
- Václavík, T., and R. K. Meentemeyer. 2009. Invasive species distribution modeling iSDM: Are absence data and dispersal constraints needed to predict actual distributions? *Ecological Modelling* 220: 3248–3258.
- Václavík, T., and R. K. Meentemeyer. 2012. Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. *Diversity and Distributions* 18:73–83.
- Van Wilgen, B. W., D. M. Richardson, D. C. Le Maitre, C. Marais, and D. Magadlela. 2001. The economic consequences of alien plant invasions: examples of impacts and approaches to sustainable management in South Africa. *Environment Development and Sustainability* 3:145–168.
- Van Wilgen, B. W., et al. 2011. National-scale strategic approaches for managing introduced plants: insights from Australian acacias in South Africa. *Diversity and Distributions* 17:1060–1075.
- Walther, G. R., et al. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution* 24:686–693.
- Wan, J.-Z., C.-J. Wang, and F.-H. Yu. 2016. Risk hot-spots for terrestrial plant invaders under climate change at the global scale. *Environmental Earth Sciences* 75:1–8.
- Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. Davis. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Science USA* 105:17029–17033.
- Willis, C. G., et al. 2010. Favourable climate change response explains non-native species' success in Thoreau's Woods. *PLoS ONE* 5:e8878.
- Winter, M., et al. 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Science USA* 106: 21721–21725.
- Wisz, M. S., et al. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14:763–773.
- Zachariades, C., J. H. Hoffmann, and A. P. Roberts. 2011. Biological control of mesquite *Prosopis* species Fabaceae in South Africa. *African Entomologist* 19:402–415.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1694/full>