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BIODIVERSITY RESEARCH

Modelling horses for novel climate courses: insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models

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ABSTRACT

Aim Investigate the relative abilities of different bioclimatic models and data sets to project species ranges in novel environments utilizing the natural experiment in biogeography provided by Australian *Acacia* species.

Location Australia, South Africa.

Methods We built bioclimatic models for *Acacia cyclops* and *Acacia pycnantha* using two discriminatory correlative models (MaxEnt and Boosted Regression Trees) and a mechanistic niche model (CLIMEX). We fitted models using two training data sets: native-range data only ('restricted') and all available global data excluding South Africa ('full'). We compared the ability of these techniques to project suitable climate for independent records of the species in South Africa. In addition, we assessed the global potential distributions of the species to projected climate change.

Results All model projections assessed against their training data, the South African data and globally were statistically significant. In South Africa and globally, the additional information contained in the full data set generally improved model sensitivity, but at the expense of increased modelled prevalence, particularly in extrapolation areas for the correlative models. All models projected some climatically suitable areas in South Africa not currently occupied by the species. At the global scale, widespread and biologically unrealistic projections by the correlative models were explained by open-ended response curves, a problem which was not always addressed by broader background climate space or by the extra information in the full data set. In contrast, the global projections for CLIMEX were more conservative. Projections into 2070 indicated a polewards shift in climate suitability and a decrease in model interpolation area.

Main conclusions Our results highlight the importance of carefully interpreting model projections in novel climates, particularly for correlative models. Much work is required to ensure bioclimatic models performed in a robust and ecologically plausible manner in novel climates. We explore reasons for variations between models and suggest methods and techniques for future improvements.

Keywords

Bioclimatic model, biological invasions, correlative model, fundamental niche, invasion dynamics, Köppen–Geiger climate zone, mechanistic niche model, modelling methods, realized niche, species distribution model.

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INTRODUCTION

Understanding the potential impacts of novel climates on native and alien species distributions is critical for conservation planning and management, but projecting ecological futures is highly uncertain. Studies that model species ranges can encounter methodological, conceptual and theoretical difficulties, making interpretation of results problematic for both current and future environments (Dormann, 2007; Coreau *et al.*, 2009; Rodda *et al.*, 2011).

Bioclimatic models are commonly used for projecting the potential range of invasive species for risk assessment and more generally for species range shifts under the influence of climate change (Guisan & Zimmermann, 2000; Kriticos & Randall, 2001). These models define the potential limits of species distributions using various combinations of the species known range, physiological tolerances, biotic interactions and dispersal potential (Elith & Leathwick, 2009; Kearney & Porter, 2009; Soberón & Nakamura, 2009). The models are then transferred or projected to other regions or times to identify additional areas suitable for occupation by the species in question.

The most commonly used bioclimatic models are correlative, linking readily available species distribution records with spatial environmental data, using either statistical or machine learning techniques (Elith & Leathwick, 2009). An alternative, but more time- and data-intensive approach is to link the ecophysiological responses of species to environmental covariates in mechanistic bioclimatic models (Kriticos & Randall, 2001; Sutherst, 2003; Kearney & Porter, 2009).

Which components of the species niche are represented in different modelling techniques depends on the framing of the research question (Venette *et al.*, 2010), the modelling method and the training data used (Kearney, 2006; Hirzel & Le Lay, 2008; Soberón & Nakamura, 2009). These choices, in turn, can influence model projections. Novel climates are key areas of interest for invasion ecology and climate change, as well as for the management and policy frameworks built on such knowledge. The three primary determinants of a species range are climate, biotic interactions and dispersal (Soberón & Nakamura, 2009). Because biotic and dispersal drivers of distributions can change rapidly owing to anthropogenic influences, the goal for bioclimatic models exploring habitat suitability in novel climates should be to approximate the Grinnellian fundamental niche (*sensu* Soberón, 2007). At the very least, they should be able to characterize the realized Hutchinsonian niche (*sensu* Soberón, 2007) underlying the species' native range.

Various approaches aim to develop bioclimatic models that more closely approximate fundamental niches, while recognizing that perfect matches are not possible. Theoretically, the ability of correlative and mechanistic models to project suitable novel climate space should be improved by greater model complexity and the inclusion of more species-relevant data, but this construct is rarely tested. For example, mechanistic models are potentially able to get closer to understanding the determinants of the fundamental niche by considering ecophysiological processes. Alternatively, it has been suggested that models of invasive species fitted with pooled data from alien and native ranges may improve the descriptive performance of the models relative to models fitted with native-range data only (Mau-Crimmins *et al.*, 2006; Broennimann & Guisan, 2008; Sanchez-Fernandez *et al.*, 2011). Current consensus suggests that correlative model outputs align more closely with species' realized distributions, while mechanistic models more closely approximate their fundamental climate niche and therefore robustly project species ranges into novel climates (Soberón, 2010; Rodda *et al.*, 2011). Yet few studies have rigorously investigated or tested this proposition (but see Sutherst & Bourne, 2009; Elith *et al.*, 2010; Kearney *et al.*, 2010).

The expertise and resources required to parameterize mechanistic models may not be available for many species, thus limiting their application to high profile questions. In contrast, correlative models are quick to parameterize, have minimal requirements and use widely available species distribution records and spatial environmental data. It is therefore highly likely that they will continue to be used. Concerns about extrapolation issues (e.g. Sutherst & Bourne, 2009) have prompted some authors to argue for careful and critical evaluation of the performance of correlative models in novel environments to identify and address problems requiring resolution (Elith *et al.*, 2010; Venette *et al.*, 2010; Rodda *et al.*, 2011).

Acacia cyclops A.Cunn. ex G.Don and *Acacia pycnantha* Benth. (subgenus *Phyllodineae*, Mimosoideae: Fabaceae; Miller *et al.*, 2011) are native to Australia and major invasive species in South Africa, the Iberian Peninsula and California (Turpie *et al.*, 2003; Gaertner *et al.*, 2009; Le Maitre *et al.*, 2011; Richardson & Rejmánek, 2011). The life histories of both species are well characterized, and their native and naturalized distributions, well documented (see review in Appendix S2 in Supporting Information). In Australia, both species have become naturalized outside their historical native distributions (Maslin & McDonald, 2004). In South Africa, both species had been introduced by the mid-19th century and widely planted for land rehabilitation and commercial purposes. This long invasion history, widespread colonization and well-documented distributions may be viewed as a 'natural experiment in biogeography' from which much can be learnt about species range dynamics (Richardson *et al.*, 2011). This makes these *Acacia* species useful model systems for comparing the ability of different approaches to project potential geographic ranges for species in novel environments. As such, Australian acacias in South Africa provide a unique opportunity to investigate tools for invasive species and climate change risk assessment.

In this study, we compare the ability of different modelling methods to make projections of species potential ranges in novel environments. Because we cannot test this directly, beyond qualitative assessments based on theoretical expectations, we use invasions of novel environments in South Africa as a proxy for future novel climates. Specifically, we built bioclimatic models for *A. cyclops* and *A. pycnantha* using the mechanistic niche model CLIMEX (Sutherst & Maywald, 1985; Sutherst *et al.*, 2007) and two discriminative correlative modelling techniques MaxEnt (Phillips *et al.*, 2006) and Boosted Regression Trees (BRT; Ridgeway, 2007; Elith *et al.*, 2008). We fitted models for the three techniques utilizing two training data sets: native-range data only ('restricted') and all available global data excluding South African distribution records ('full'). We compared the ability of the six techniques (three *bioclimatic models* × two *training data sets*) to project the climate suitability for observed records of the two species in South Africa. In addition, we assessed the impacts of climate change on the potential distributions of the two species in both native and alien habitats. Our intention is to motivate developments that improve bioclimatic modelling of novel climates by investigating what differences in the models or training data sets are responsible for variation in model behaviour. Finally, we explore how correlative and mechanistic modelling approaches can complement each other or, together, facilitate the development of more robust bioclimatic modelling techniques.

METHODS

Study species and area

Acacia cyclops was introduced at least twice to South Africa (1845 from Australia, 1895 secondarily from France) for drift-sand stabilization purposes (Shaughnessy, 1980, 1986; Poynton, 2009; see discussion in Le Roux *et al.*, 2011). Since introduction, *A. cyclops* has spread rapidly and currently occurs throughout the western and south-western coastal region of South Africa. In its native range, *Acacia cyclops* is a shrub to 4 m (−6 m) high, found along the coast of the south-west of Western Australia (SWWA) and South Australia and inland up to 60 km in areas with winter rainfall and mild to warm and dry summers (Gill, 1985).

Acacia pycnantha is a shrub or tree up to 10 m tall (Maslin & McDonald, 2004), is the Australian national flora emblem, is long established in cultivation and was introduced in the 19th C from its native range in south-eastern Australia to both SWWA and the Cape Floristic Region (CFR; Boucher & Stirton, 1978). In Australia, it has extended its native range since European settlement in both New South Wales (NSW) and wetter parts of Victoria (Maslin, 2001), and naturalized alien populations occur in NSW, SWWA and eastern Tasmania (Maslin, 2001). Its combined native and alien distribution in Australia extends from regions with Mediterranean to temperate climates. In the CFR, *A. pycnantha* has been introduced at least twice, both times from Australia and presumably in low numbers for dune stabilization, tan bark production and ornamental purposes (Poynton, 2009). Between 22 and 29 million seeds were subsequently locally sourced in South African plantations for distribution to the eastern parts of the country (Stirton, 1978; Poynton, 2009; see discussion in Le Roux *et al.*, 2011).

We compiled species distribution data from a variety of sources. For Australia, we sourced location records from various Australian state and territory herbaria via the Australian Virtual Herbarium online database (http://www.ersa.edu.au/avh), the Centre for Invasion Biology, Stellenbosch University (C·I·B) database on introduced species and the database of Seeding Victoria (A. Pearson and A. Ovington, unpubl. data.) for *A. pycnantha*. For South Africa, we obtained location records from the C·I·B database, the South African Plant Invaders Atlas (AGIS, 2007) and the National Herbarium Pretoria Computerized Information System (PRECIS; Appendix S1). For other global distribution data, records were sourced from the GBIF online database (http://data.gbif.org), from the scientific literature and from scientists involved in invasive species management (see acknowledgements). Because of the greater uncertainty associated with these records, relative to native-range data and our South African records, we spent longer scrutinizing these data and generally cross-checked information using more than one source.

Records were scrutinized with the help of expert consultation (Bruce Maslin, Department of Environment & Conservation W.A. and Phillip Kodela, Royal Botanic Gardens Sydney, for Australia; Lesley Henderson, Plant Protection Research Institute, for South Africa) to remove misidentified, revised, cultivated or suspected inaccurate or imprecise records (Table 1). We further scrutinized records in environmental space relative to model background data using box and whisker plots for each Bioclim variable (Fig. S1). Records that were obvious outliers were further investigated and removed if the location and other evidence indicated that they were growing in managed environments. We separated naturalized alien records of the two *Acacia* taxa within Australia from native-range records (Figs 1 & 2). In the South African SAPIA and PRECIS databases, locations were recorded on a 1 min, 5 min or 0.25° square grid. Where possible, the latter records were located more accurately using the locality descriptions, and duplicate records were removed, where possible (see Appendix

Table 1 Distribution record processing for *Acacia cyclops* and *Acacia pycnantha* modelling.

Data set	Type	*Acacia cyclops*	*Acacia pycnantha*
Restricted (R)	Raw	791	1958
	Cleaned	202	1338
	Regularized	103	497
Full (F)	Raw	1139 (791, 167, 181)	2193 (1958, 171, 64)
	Cleaned	432 (202, 161, 69)	1500 (1338, 144, 18)
	Regularized	172 (103, 29, 40)	563 (497, 51, 15)
South Africa	Raw	1516	452
	Cleaned	590	139
	Regularized	234	59

Restricted data set includes only native-range distribution records. Full data set includes the total of native, alien Australian and alien global (excluding South Africa) distribution records (listed in that order in parentheses). Regularized data represent data used in the correlative models, where only one record is retained per 10' CliMond climatology grid cell.

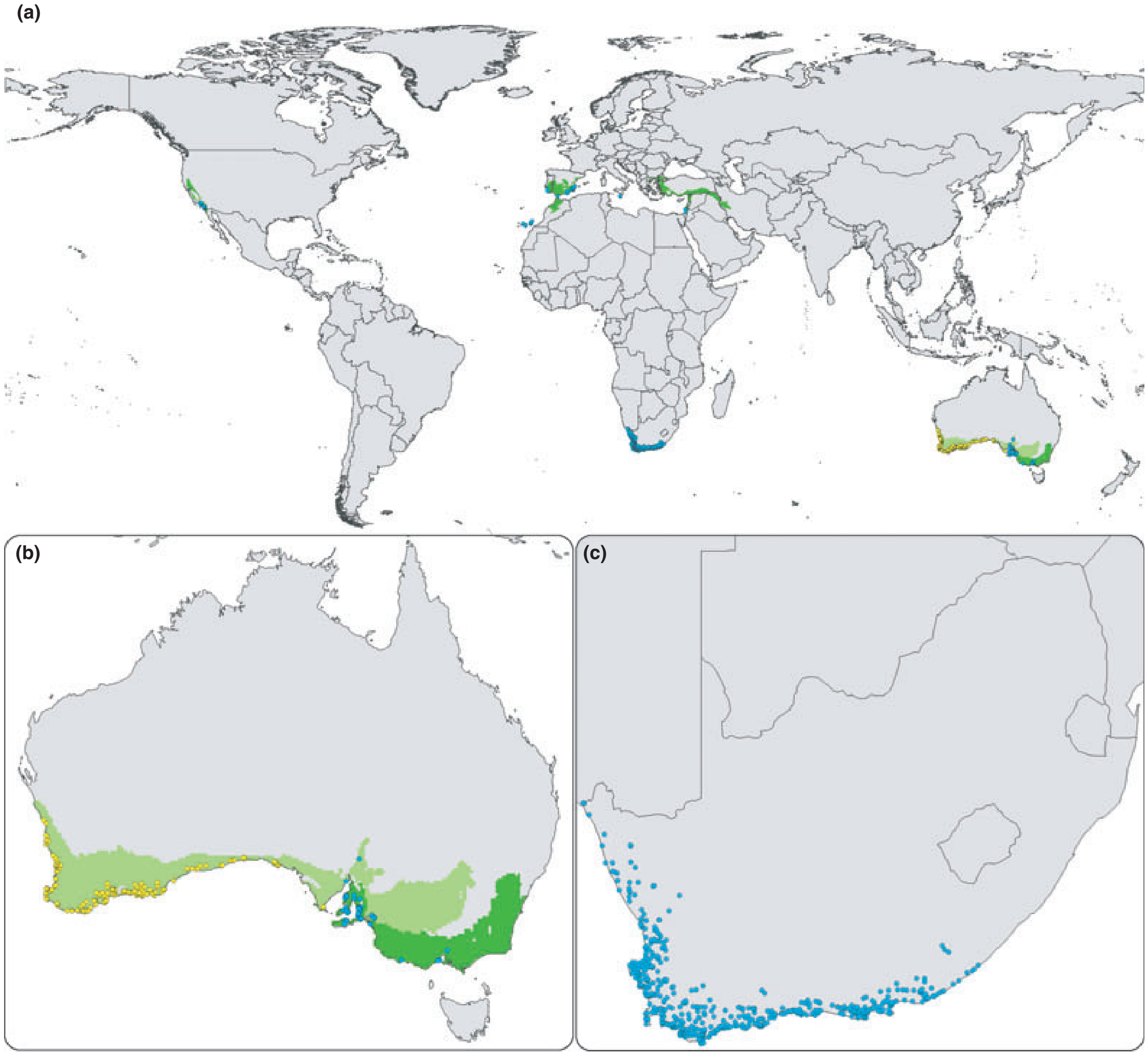


Figure 1 The known global distribution of *Acacia cyclops*. Distribution record data for native (light yellow circles) and naturalized alien (dark blue circles) populations are indicated against correlative model backgrounds for restricted (light green shading) and full (light green plus dark green shading) training data sets globally (a) and in greater detail for Australia (b) and South Africa (c).

S1 for further methods). The data cleaning reduced the number of available records considerably (Table 1). For the correlative models, we further reduced the number of records to one per 10′ grid cell (regularized data) to minimize sampling bias (Table 1; Phillips *et al.*, 2009). For *A. cyclops*, the regularized data represented 13% and 15% of the raw data records, whereas for *A. pycnantha*, they represented 25% and 26% of the raw data records (in both cases for full and restricted training data sets, respectively).

Climate data and future projections

Steep climatic gradients in the Western Cape region of South Africa demanded a finer-scale climatology data set for modelling than the 0.5° data sets previously available to CLIMEX (Sutherst *et al.*, 2007). We used the CliMond 10′ gridded climate data (Kriticos *et al.*, 2011) for all modelling approaches, ensuring climate data uniformity between models. The CliMond data set uses updated equations for calculating humidity values, relative to the CRU 10′ data (New *et al.*, 2002), and addresses missing data present in the WorldClim precipitation layers and change surfaces (Hijmans *et al.*, 2005). Historical climate (averaging period 1950–2000) was represented using average minimum monthly temperature (T_{min}), average maximum monthly temperature (T_{max}), average monthly precipitation (P_{total}) and relative humidity at 09:00 h ($RH_{09:00}$) and 15:00 h ($RH_{15:00}$). Potential future climate at 2070 was represented by the same five variables

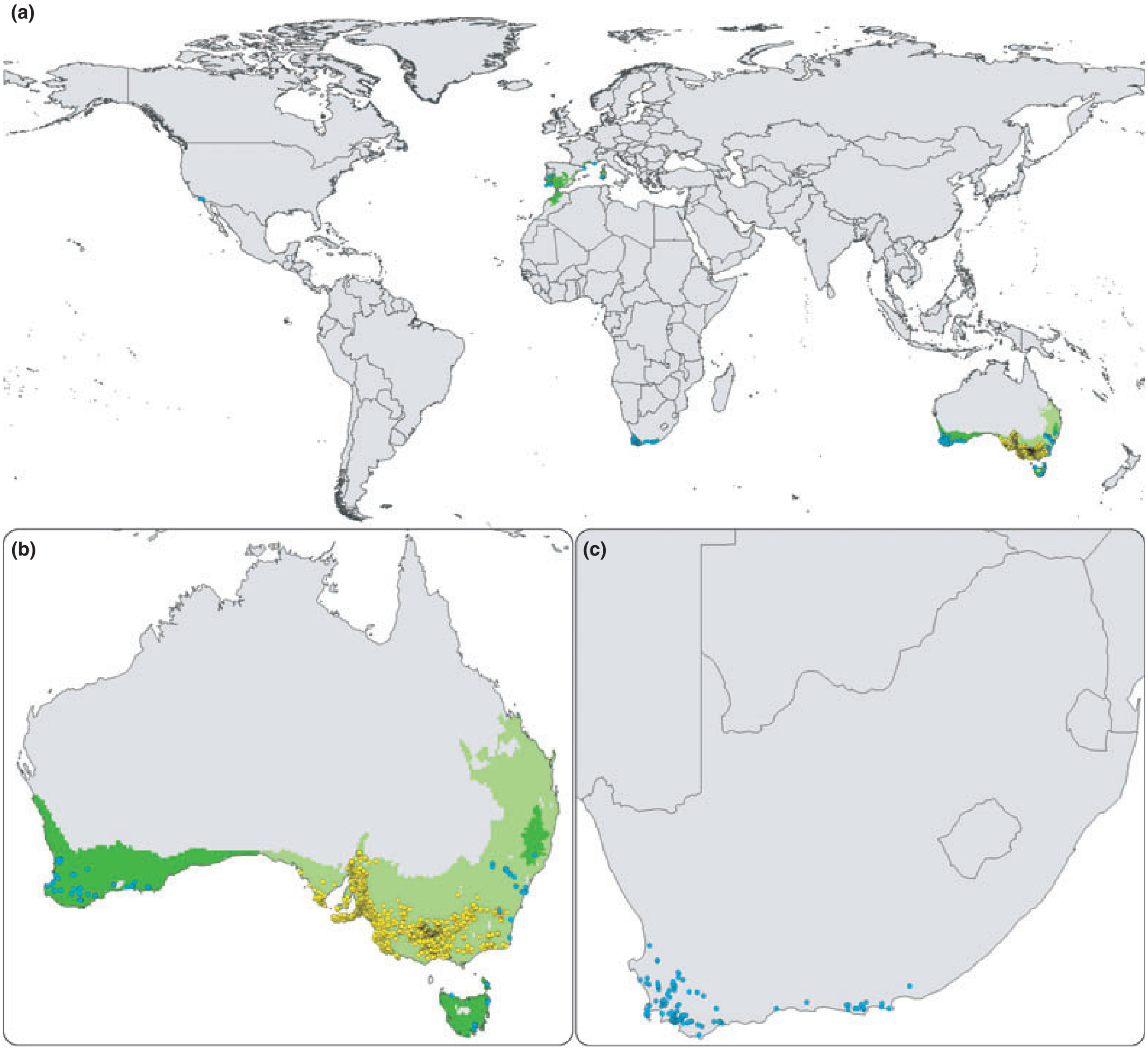


Figure 2 The known global distribution of *Acacia pycnantha*. Distribution record data for native (light yellow circles) and naturalized alien (dark blue circles) populations are indicated against correlative model backgrounds for restricted (light green shading) and full (light green plus dark green shading) training data sets globally (a) and in greater detail for Australia (b) and South Africa (c).

using the CSIRO-Mk3.0 (Gordon *et al.*, 2002) global climate model with the A1B SRES emission scenarios (IPCC, 2000), available as part of the CliMond data set.

For correlative modelling, we chose five CliMond variables *a priori* that best represent the ecological stress factors in the native ranges of the two study taxa and that are most equivalent to the stress variables used to parameterize the CLIMEX models. The five bioclimatic variables were mean temperature of the warmest quarter (Bio10; cf hot stress), mean temperature of the coldest quarter (Bio11; cf cold stress), mean moisture index of the driest quarter (Bio33; cf dry stress), mean moisture index of the warmest quarter (Bio 34; cf hot and dry stress) and mean moisture index of the coldest quarter (Bio 35; cf cold and dry stress). We examined colinearity among the five variables within the backgrounds used to train the correlative models for the two *Acacia* species. In most cases, correlations between chosen Bioclim variables were weak ($-0.6 < r < 0.6$) except for Bio33 and Bio34 (Ac.R and Ap.R), Bio10 and Bio35 (Ap.R) and Bio30 and Bio34 (Ap.F and Ac.F), which had strong correlations ($r < -0.8$, $r > 0.8$) for some but not all data sets (for abbreviations used, please see the following paragraph).

Species distribution modelling

We applied three bioclimatic models to *A. cyclops* (Ac) and *A. pycnantha* (Ap): two correlative models (MaxEnt, M; Boosted Regression Trees, B) and one mechanistic niche model

(CLIMEX, C). We built models for two training data sets: native-range data only ('restricted', R) and all available global data, excluding South African distribution records ('full', F; see Appendix S2 for detailed record information). For CLIMEX models, the full data set included biological and ecophysiological information in addition to alien species distribution records (Appendix S2). All three models were projected globally using historical (1975H) and modelled future (2070) climate data, but statistical comparisons among models were restricted to (1) the species distribution records used for model construction within the region defined by the correlative model backgrounds and (2) independent species distribution records in South Africa.

Correlative species distribution modelling

We used MaxEnt version 3.3.3e (Phillips *et al.*, 2006) and Boosted Regression Trees version 1.6-3 (Ridgeway, 2007; Elith *et al.*, 2008) to fit the restricted and full training data sets to historical climate conditions, and subsequently made spatial projections globally under historical climate conditions and the 2070 climate change scenario.

MaxEnt relies on a user-defined geographical background for sampling the climate of a reference set of grid cells for comparison with the climate of grid cells where the species is present. The definition of the background data set can influence significantly the model results (VanDerWal *et al.*, 2009; Elith *et al.*, 2011). Conceptually, the background should include the full environmental range of the species including those areas that are reachable and have been searched (Elith *et al.*, 2010). One method of choosing a background is to use a minimum convex polygon drawn around the presence points. A less arbitrary method is to use regionally based biophysical classifications, for example, agroclimatic zones in Australia (Hobbs & McIntyre, 2005) or biomes in southern Africa (Rutherford, 1997). We required a classification that could be applied globally. There are several such classifications, from which we chose the Köppen–Geiger classification because it classes Earth's climate into zones based on vegetation, precipitation and temperature with class boundaries specifically chosen to match large-scale vegetation changes (Köppen, 1936). We spatially intersected distribution records for both *Acacia* species with Köppen–Geiger climate zones provided with the CliMond 10′ historical climate data (Kriticos *et al.*, 2011). Köppen–Geiger polygons containing one or more species records were included in the background, and separate backgrounds were produced for the restricted and full training data sets (Figs 1 & 2).

For all four model combinations, we used the default settings in MaxEnt version 3.3.3e with the exception that we restricted model building to hinge features and used the additional options of 'create response curves' (response curves were clamped) and 'perform jack-knife'. We restricted our models to using hinge features because they 'allow simpler and more succinct approximations of the true species response to the environment' (Phillips & Dudík, 2008, p. 173). Elith *et al.* (2010) also found that hinge features produced model projections more congruent with those from a mechanistic ecophysiological model for the invasive cane toad in Australia.

Unlike MaxEnt, which uses species presence records and background area for comparison, BRT models require both species presence and absence or background records. Using the same background area as the MaxEnt models for both *Acacia* species, we transformed the restricted and full occurrence records into presence/background grids with each grid cell within the background area given a '1' where one or more presence records fell within the cell and '0' otherwise. Presence to background data counts using the restricted training data set for *A. cyclops* were 103:2424 (total 2527), for *A. pycnantha*, 497:3746 (total 4243), and for the full training data set, 172:6623 (total 6795) and 563:6810 (total 7374), respectively. The BRT models were fitted using the Generalized Boosted Regression Models package (GBM version 1.6-3; Ridgeway, 2007) and run in the R-statistics package version 2.10.1 (R Development Core Team 2010) using the customized R code provided in the Elith *et al.* (2008) supplementary material tutorial. To avoid biasing the model with relatively large ratios of presences to background, the data were weighted so that the sum of the weighted presences equalled the sum of the weighted background. The models were initially tested using the entire background and random 50% and 25% samples from the background. This was found to have almost no effect on the model results. We therefore used the entire background to keep the inputs the same as those for MaxEnt. The model was run with a bag (training subsample) size of 50% and with the default 10-fold cross-validation. The default values suggested by Elith *et al.* (2008) for tree complexity (smoothness) and the learning rate were applied and then modified to give varying numbers of trees, so that errors were minimized and overfitting was avoided. Varying settings for tree complexity and learning rate were used to obtain about 1000–2000 fitted trees. Increasing the tree complexity allows the model to better represent interactions between the variables. However, the model statistics and visual comparisons of the outputs showed that increasing tree complexity resulted in poorer fits to the modelled species localities and typically increased the extent of the projected highly suitable areas globally. We therefore adopted a tree complexity of 1 throughout. For *A. pycnantha*, the final model for the restricted training data set used a learning rate of 0.01, which resulted in 1600 trees giving the optimal fit; for the full training data set, the learning rate was 0.03, which gave 950 trees. For *A. cyclops*, the learning rate was 0.002 for the restricted data set, which gave an optimal fit with 1500 trees; for the model trained with the full data set, the learning rate was 0.1, which gave 1000 trees.

Interpreting correlative species distribution models

Mapped projections and response functions were visually assessed for features that might indicate causes for concern. Additionally, to define where models were extrapolating or interpolating, multivariate environmental similarity surfaces

(‘MESS’ maps *sensu* Elith *et al.*, 2010) were calculated by comparing the models’ reference climates (defined as species background regions) with the projection region, under historical and future climate scenarios using MaxEnt version 3.3.3e. This new feature of MaxEnt calculates a climatic similarity measure comparable to that in a BIOCLIM model but extended to differentiate levels of dissimilarity as negative values (Elith *et al.*, 2010). A threshold of zero for values from MESS surfaces was used to create mask overlays of negative values for each model, highlighting areas that represent novel climate space relative to the range under which the model was fitted and therefore where the model is extrapolating (MESS−) rather than interpolating (MESS+).

Mechanistic modelling

Mechanistic modelling was performed using CLIMEX version 3 (Sutherst & Maywald, 1985; Sutherst *et al.*, 2007). CLIMEX is a process-oriented ecophysiological niche model that combines inferential and deductive modelling approaches to describe the species response to climatic variables, and to use this model to estimate its potential geographical distribution. CLIMEX uses a database of five meteorological variables ($T_{\min}$, $T_{\max}$, P_{total}, $RH_{09:00}$ and $RH_{15:00}$) to derive weekly and annual indices that define the species response to temperature and soil moisture. The potential for population growth is described by a weekly growth index (GI_W), which is integrated to create the annual growth index (GI_A). Weekly stress indices (cold, hot, wet, dry and, in some cases, their interactions) can be used to define the ability of a population to survive inclement conditions (Sutherst *et al.*, 2007). Growth indices accord with the Sprengel–Liebig law of the minimum and Shelford’s law of tolerance (Shelford, 1963; van der Ploeg *et al.*, 1999), while stress indices accord with widely observed patterns of species population response to stressful conditions.

In CLIMEX, species range boundaries are mostly defined by climatic stresses (Sutherst, 2003). The models use input values for the response parameters from multiple sources, for example geographical distribution records, ecophysiological studies of growth or survival or phenological observations. For restricted training data sets, we used the approach of fitting model parameters to native distribution records, with some consideration of ecophysiological principles such as the soil moisture index value that corresponds with permanent wilting point, but no consideration of ancillary knowledge of the species’ ecology. This is not the standard method for building a CLIMEX model (Sutherst *et al.*, 2007; Sutherst & Bourne, 2009), but we were interested in the relative performances of models built with comparable data sets. For models trained with the full data sets, we used the recommended approach that utilizes all available data sources to set response parameters and stresses (Sutherst & Bourne, 2009). Table S1 lists the parameter values used in this study for *A. cyclops* and *A. pycnantha* based on supporting evidence detailed in Appendix S2.

CLIMEX growth and stress indices are integrated into a single annual measure of overall climatic suitability, the ‘Ecoclimatic Index’ (EI; scaled from 0 to 100). The EI value provides an overall indication of the modelled climatic suitability of a given location (Sutherst *et al.*, 2007). Establishment is only possible when EI > 0. In practice, EI values close to the maximum are rare as this would imply ideal growth conditions year-round (Sutherst, 2003). The contributing components of EI can be examined to better understand a species climatic response for any given location (Sutherst *et al.*, 2007).

Intermodel comparison and goodness-of-fit

The probabilistic measures of environmental suitability used by MaxEnt and BRT are not directly comparable with EI values in CLIMEX. Model comparison and validation was facilitated by defining a threshold above which model projections are considered to be suitable for the species (Pearson *et al.*, 2007). There are many ways of setting thresholds with correlative model projections (see Liu *et al.*, 2005), and the choice depends on the model purpose (Lobo *et al.*, 2008). The lowest presence threshold (LPT) is the lowest output value for an observed presence record and can be interpreted ecologically as representing climatic conditions at least as suitable as those where the species has been recorded (Pearson *et al.*, 2007). Because LPT minimizes omission errors, it is particularly suitable for invasive species risk analysis, where the consequences of a false negative generally outweigh those of a false positive. The LPT can also be identified for both the correlative models and CLIMEX (Table 2). For CLIMEX, we manually set the LPT to 1 because of the ecological equivalency of this EI value to the LPT (Sutherst *et al.*, 2007; in practice, 1 was the projected LPT for 6 of the 8 CLIMEX models). For each model, we converted suitability indices in each grid cell to presence (suitable) and absence (unsuitable) values using LPT.

Assessing the goodness-of-fit of models for which we only have presence data is particularly challenging (Zaniewski *et al.*, 2002; Elith *et al.*, 2006). The majority of statistical methods for assessing the goodness-of-fit of species distribution models and niche models measure the ability of the model to discriminate between an in-class and an out-class for both model results and input locations. Where information on habitat unsuitability is not available, which is usually the case, modellers typically rely upon pseudo-absences (locations assumed to be unsuitable for the species being modelled). The statistical methods assess how well the model is able to discriminate between the known presences and the assumed absences, often using cross-validation to test the predictions on a portion of the data set not included in the fitted model (e.g. AUC, Cohen’s kappa). More recently, the concept of the model background has been introduced in an attempt to overcome some of the obvious problems with using pseudo-absences (Phillips *et al.*, 2006).

Ideally, an invasive species risk model should encompass all of the test locations. This attribute is known as the model *sensitivity*, or the proportion of all test locations correctly modelled as occurring in climatically suitable areas. Low model sensitivity increases the likelihood of underestimating an invasive species risk, so models with very high sensitivity

Table 2 Intermodel comparison and goodness-of-fit measures for *Acacia cyclops* and *Acacia pycnantha* bioclimatic models projected with recent historical climate data (1975H).

				LPT			Suitable area ($km^2 \geq$ LPT)			Modelled prevalence			Sensitivity		
Species	Training data set	DR	RP	M	B	C*	M	B	C	M	B	C	M	B	C
Ac	R	R	R	0.096	0.322	1	235568	177781	650590	0.32	0.24	0.90	1.00	1.00	1.00
Ap	R	R	R	0.029	0.127	1	816605	474415	761173	0.68	0.40	0.64	1.00	1.00	1.00
Ac	F	F	F	0.012	0.128	1	1273056	701842	1351808	0.66	0.36	0.71	0.99	0.99	1.00
Ap	F	F	F	0.034	0.042	1	1510128	1626366	1690224	0.73	0.79	0.81	1.00	1.00	0.98
Ac	R	RSA	RSA	0.096	0.322	1	462065	435665	74271	0.36	0.34	0.06	0.96	0.84	0.46
Ap	R	RSA	RSA	0.029	0.127	1	384072	371158	349954	0.31	0.29	0.28	0.98	0.85	0.97
Ac	F	RSA	RSA	0.012	0.128	1	855603	622472	706062	0.66	0.48	0.55	1.00	0.97	0.94
Ap	F	RSA	RSA	0.034	0.042	1	704487	874855	737655	0.56	0.69	0.57	1.00	1.00	1.00
Ac	R	All	World	0.096	0.322	1	49316931	54687645	1571261	0.27	0.32	0.01	0.92	0.93	0.66
Ap	R	All	World	0.029	0.127	1	44330218	28384190	9020993	0.44	0.25	0.06	0.99	0.95	0.98
Ac	F	All	World	0.012	0.128	1	57802202	64656503	7303886	0.31	0.35	0.04	1.00	0.98	0.96
Ap	F	All	World	0.034	0.042	1	57337283	69195197	8443825	0.55	0.62	0.05	1.00	1.00	0.98

*Manually set. RP, region of projection; DR, distribution record data; LPT, lowest presence threshold; M, MaxEnt; B, Boosted Regression Trees; C, CLIMEX; Ac, *Acacia cyclops*; Ap, *Acacia pycnantha*; R, restricted data set; F, full data set (including background region and test records); RSA, South Africa within the mainland political boundaries (i.e. excluding Lesotho and Swaziland); All, F + RSA.

should be preferred. However, model sensitivity alone does not indicate how useful the model is. A model that encompasses the entire globe would have perfect sensitivity, but be of little use. The natural complement of sensitivity is *specificity*, the proportion of true absences occurring in climatically unsuitable areas. A more specific model has fewer commission errors. In the absence of reliable measures of habitat unsuitability (i.e. true absence data), we had to use a proxy. *Modelled prevalence* is the proportion of the model universe (i.e. the region being projected to) that is estimated to be climatically suitable, and provides the basis for identifying useful models.

One method applicable to presence-only data is to test the model sensitivity score for statistical significance (Anderson *et al.*, 2002). For small sample sizes (< 1000 records), Fisher's exact 1-tailed binomial test can be used to test the probability (P) that the sensitivity score could be achieved by chance alone given the modelled prevalence:

$$P = \sum_{i=0}^{n-k} \frac{p^{k+i}(1-p)^{[n-(k+i)]}n!}{(k+i)![n-(k+i)]!}$$

where p is modelled prevalence, k is the number of species location points falling in the modelled suitable range, and n is the total number of species location points in the sample. In this test, i is a simple counter that allows the probability to be summed for the exact case where k points out of n are correctly allocated as well as all of the more extreme cases (Zar, 1999). For larger sample sizes (> 1000), the X^2 test can be performed. Using these tests, the smaller the modelled prevalence, the lower the probability that all the presence points would be included within the suitable area by chance alone. They are therefore somewhat sensitive to the definition of the model universe.

For these tests, multiple species records within single grid cells were regularized (i.e. treated as one record), so that each grid cell was only counted once in terms of its adjacency to a known sample point and its modelled climate suitability. All the species model results were assessed for sensitivity and modelled prevalence against the relevant distribution records (DR, Figs 1 & 2; Table 2) and the region of projection (RP; Table 2).

RESULTS

Model evaluation against training data

All model projections tested against their training distribution records in their relevant training domain (i.e. the Köppen–Geiger-derived backgrounds for MaxEnt) were found to be highly statistically significant using the exact binomial test ($P < 0.0001$). Models built with the restricted training data set all achieved perfect sensitivity; though, modelled prevalence varied considerably more for the *A. cyclops* models than for the *A. pycnantha* models (Table 2). The additional distribution data contained in the full data set had a highly variable effect on the correlative model variables with respect to (1) the climate space spanned by the distribution records, (2) the amount of additional climate space spanned by background relative to the distribution records (the 'background buffering') and (3) variable range shift between the presence records relative to the variable range of the background (Fig. S1). The additional data also had no discernable effect on the ability of the models to fit closed response functions, even for response functions with considerable background buffering (Figs S2 & S3). All full training data set models for *A. cyclops* assessed against their training domain had near-perfect or perfect sensitivity scores

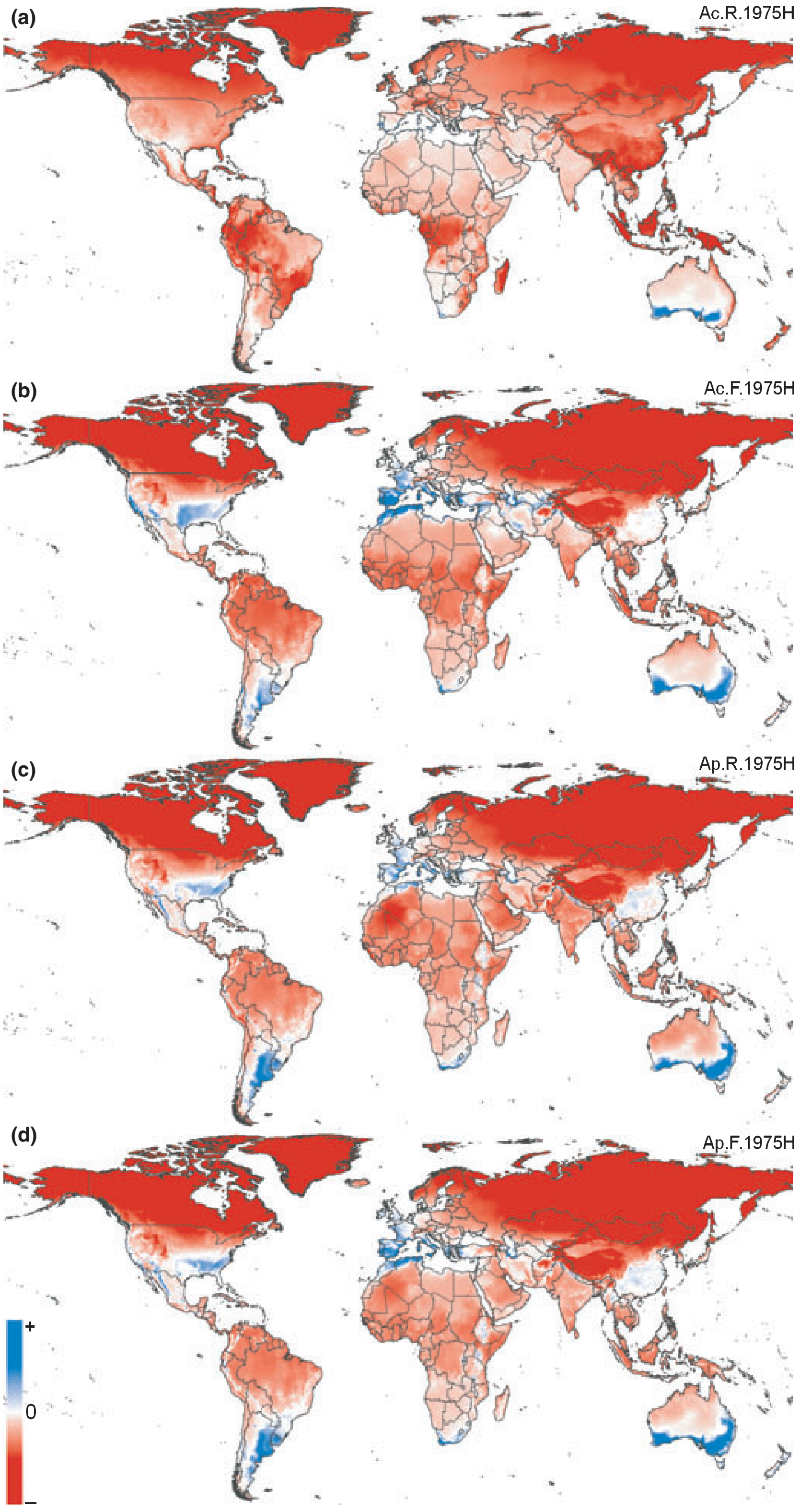
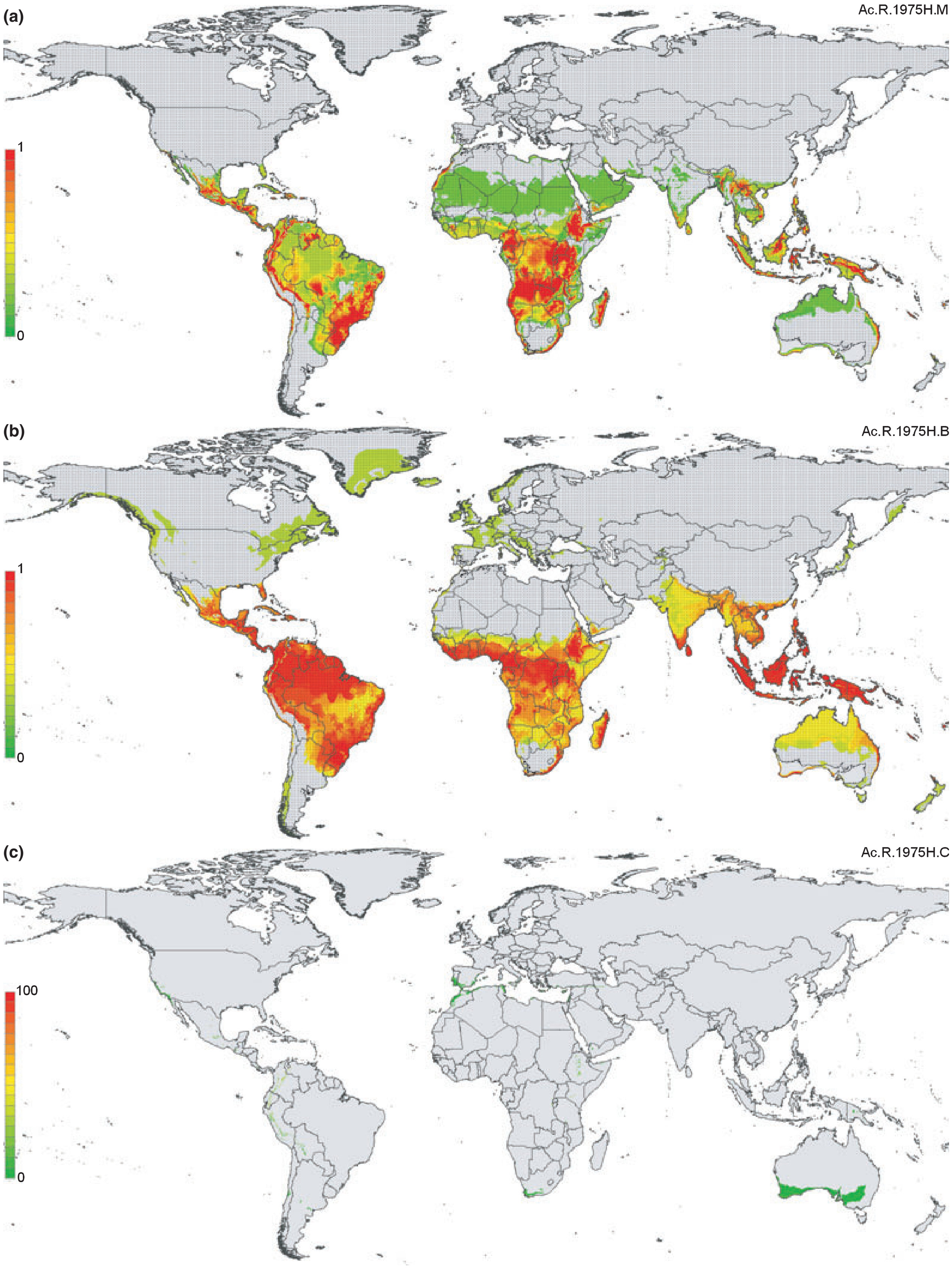


Figure 3 Multivariate environmental similarity surfaces (MESS) for *Acacia cyclops* (Ac) and *Acacia pycnantha* (Ap). Native distribution reference climates (i.e. background training domains) for restricted (R) and full (F) training data sets were compared to global climates and are depicted here for recent historical climatic conditions (1975H). Blue indicates positive values (MESS+; i.e. climatic parameters within the bounds of the reference set), and red indicates negative values (MESS−; i.e. at least one climatic parameter has a value outside the range of the reference set; novel projection climates).

Figure 4 Model projections for the potential distribution of *Acacia cyclops* (Ac) based on recent historical climates (1975H). Three models (MaxEnt, M; BRT, B; and CLIMEX, C) were applied to restricted (R) and full (F) training data sets. Colour scale indicates relative habitat suitability (MaxEnt, BRT) or climatic suitability as indicated by the CLIMEX Ecoclimatic Index (EI); these two scales are not comparable. The lower bounds of projected habitat suitability are defined by the lowest presence threshold (LPT) for each scenario (Table 2). Hashed areas define regions with negative multivariate environmental similarity surface (MESS−) values (i.e. extrapolation into novel climate space).


(a)
Ac.R.1975H.M
1
0
(b)
Ac.R.1975H.B
1
0
(c)
Ac.R.1975H.C
100
0

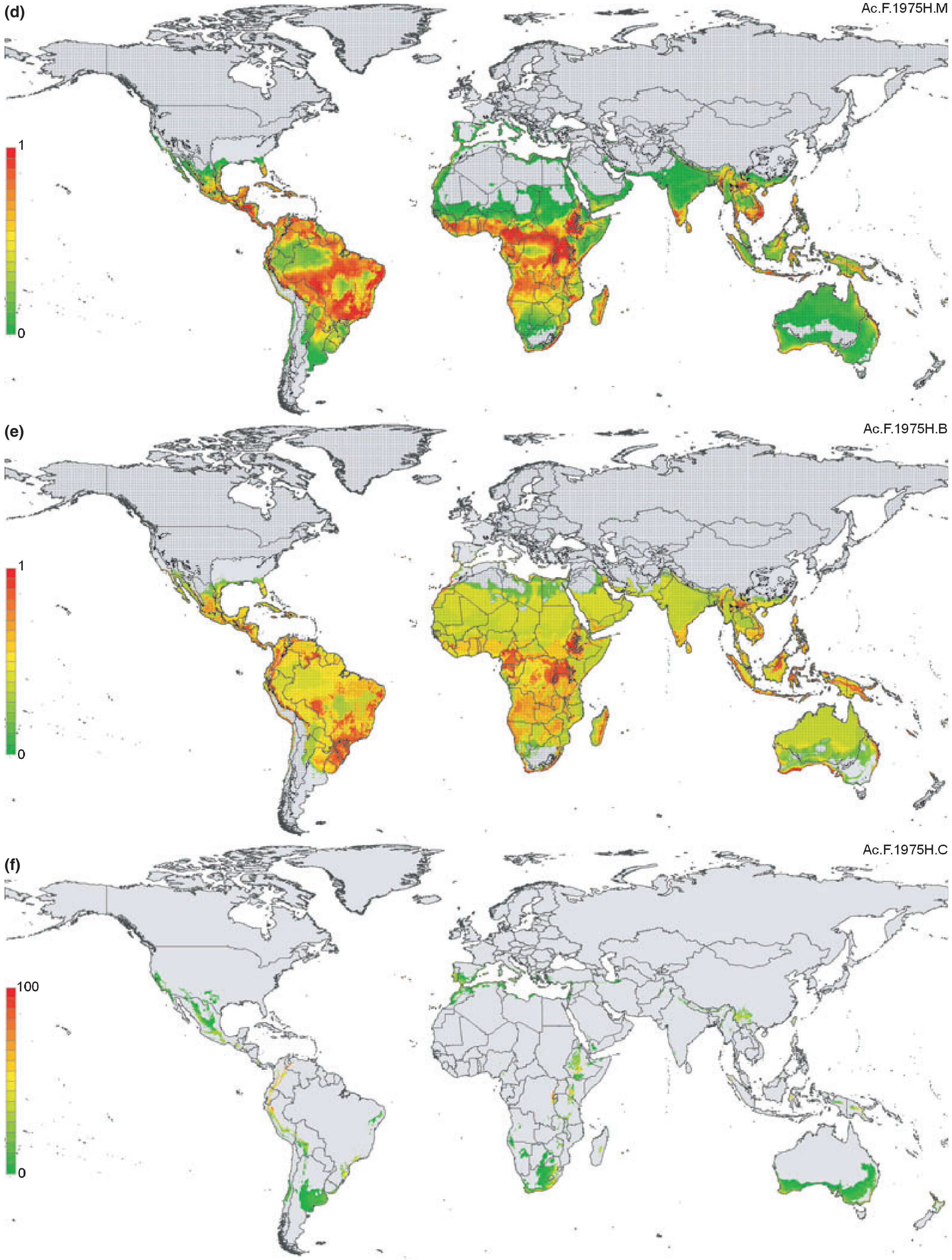


Figure 4 Continued.

(0.99–1.00). In constructing the full data set models, three records were purposefully excluded from the CLIMEX suitability projections during parameter-fitting (Appendix S2). They was the only reason the goodness-of-fit assessment did not have a perfect sensitivity. The BRT model achieved its high sensitivity score with a very small modelled prevalence (0.36) for *A. cyclops*, compared with the MaxEnt and CLIMEX models (0.66 and 0.71, respectively). Higher LPT scores for the BRT models, relative to MaxEnt models, helped by excluding large areas projected as marginally suitable. When the full data set models for *A. pycnantha* were tested against their training domain, the MaxEnt and BRT models had perfect sensitivity, while the CLIMEX model achieved a sensitivity score of 0.98. This latter value occurred because 13 distribution records were purposefully excluded when all available data were assessed while constructing the full data set CLIMEX model (see Appendix S2). Modelled prevalence was similar for all three models trained with the full data set, representing 73 – 81% of the Köppen–Geiger-derived background region.

Model evaluation against South African data

All model projections tested against the independent South African distribution records in South Africa were found to be highly statistically significant using the exact binomial test ($P < 0.0001$). However, the sensitivity and modelled prevalence results were variable (Table 2; Figs S4 & S5). For models built with the restricted data set, MaxEnt achieved high sensitivity for both species (0.96 for *A. cyclops* and 0.98 for *A. pycnantha*). For the restricted data set, most of the northern and eastern distribution records in South Africa were in extrapolation (MESS−) space for the correlative models (Figs S4 & S5). The BRT model sensitivity results were moderately poor for both species in South Africa (0.84 for *A. cyclops* and 0.85 for *A. pycnantha*). Despite perfect sensitivity in the native range, the restricted data set CLIMEX model for *A. cyclops* had a very low modelled prevalence in South Africa (0.06) and a correspondingly low sensitivity (0.46). The CLIMEX restricted data set model for *A. pycnantha* had a high sensitivity in South Africa (0.97). All three models based on the restricted data set had similar prevalence (0.28 – 0.31; Table 2). The models for *A. cyclops* developed using the full training data set had perfect (MaxEnt) or very good sensitivity (0.97, BRT and 0.94, CLIMEX). The CLIMEX model indicated that these excluded localities were excessively dry. In the South African projections for *A. cyclops*, the BRT model once again had the smallest modelled prevalence (0.48) compared with MaxEnt (0.66) and CLIMEX (0.55). The BRT model projections did not include records for *A. cyclops* in the dry interior of the Western Cape, particularly at high altitudes with low winter temperatures (Fig. S4d). The omissions in the CLIMEX models were mainly in the very arid winter rainfall areas of the north-western part of South Africa (Fig. S4f). All models for *A. pycnantha* developed using the full training data sets had perfect sensitivity in South Africa (Fig. S5), with prevalence varying between 0.56 (MaxEnt) and 0.69 (BRT; Table 2).

Model evaluation globally under historical climate

All model projections tested globally against all available data records (i.e. full data set + South African records) were found to be highly statistically significant using the exact binomial test ($P < 0.0001$). For both correlative models, much of the global projection was into extrapolation (MESS−) space (Figs 4 & 5). The Bioclim variable with the greatest influence on model projections (limiting factors *sensu* Elith *et al.*, 2010) in the MESS− space was Bio11 for both species (Fig. S8). Many response functions were open ended (that is, they maintained a high suitability value beyond the limits of the training data) resulting in substantial areas of suitable habitat within novel climates when the models were projected globally (Figs S2 & S3). In addition, no other variables reduced the modelled suitability in regions where Bio11 was the dominant variable. For *A. cyclops*, sensitivity increased for all models when the full data set was used over the restricted data set, particularly for BRT (0.83–0.98) and CLIMEX (0.66–0.96) models (Table 2). In contrast, the *A. pycnantha* models had very high sensitivity for all models and data sets (0.95–1.00). Prevalence also increased between the restricted and full data sets for all models and species. However, the biggest difference was the prevalence between the correlative models and CLIMEX (Figs 4 & 5; Table 2). The correlative models projected 27-35% and 25-62% of the global land mass as suitable, for *A. cyclops* and *A. pycnantha*, respectively. Within regions of projection interpolation for the correlative models (MESS+ areas; Fig. 3), large areas of projected suitability without distribution records generally had low climatic suitability values (Figs 4a,b & 5a,b). However, in MESS− areas, there were substantial areas of implausible medium to high climatic suitability, particularly in the tropics and subtropics for *A. cyclops* (Fig. 4a,b) and conversely in high latitudes for *A. pycnantha* (Fig. 5a,b). In contrast, the CLIMEX models produced more conservative global projections, with 1-6% of the global land mass climatically suitable (Table 2). These areas were largely restricted to Köppen–Geiger classes in which both species are recorded (Figs 4c & 5c).

Model evaluation globally under a future climate scenario

There was substantial variation among the modelling techniques and between models trained with restricted and full data sets in the area projected globally as suitable for *A. cyclops* and *A. pycnantha* under a potential future climate (2070). All models showed a polewards shift in the projected distributions, and for correlative models, a decrease in the area of model interpolation (MESS+, Figs 6, 7, S6 & S7). The polewards shift is to be expected given that projected climate change will make marginally colder areas more suitable for species that have evolved in warmer climates. At the same time, the reduction in MESS+ area indicates that an increasing proportion of the globe will experience climatic conditions that fall outside the range in the regions used in developing the

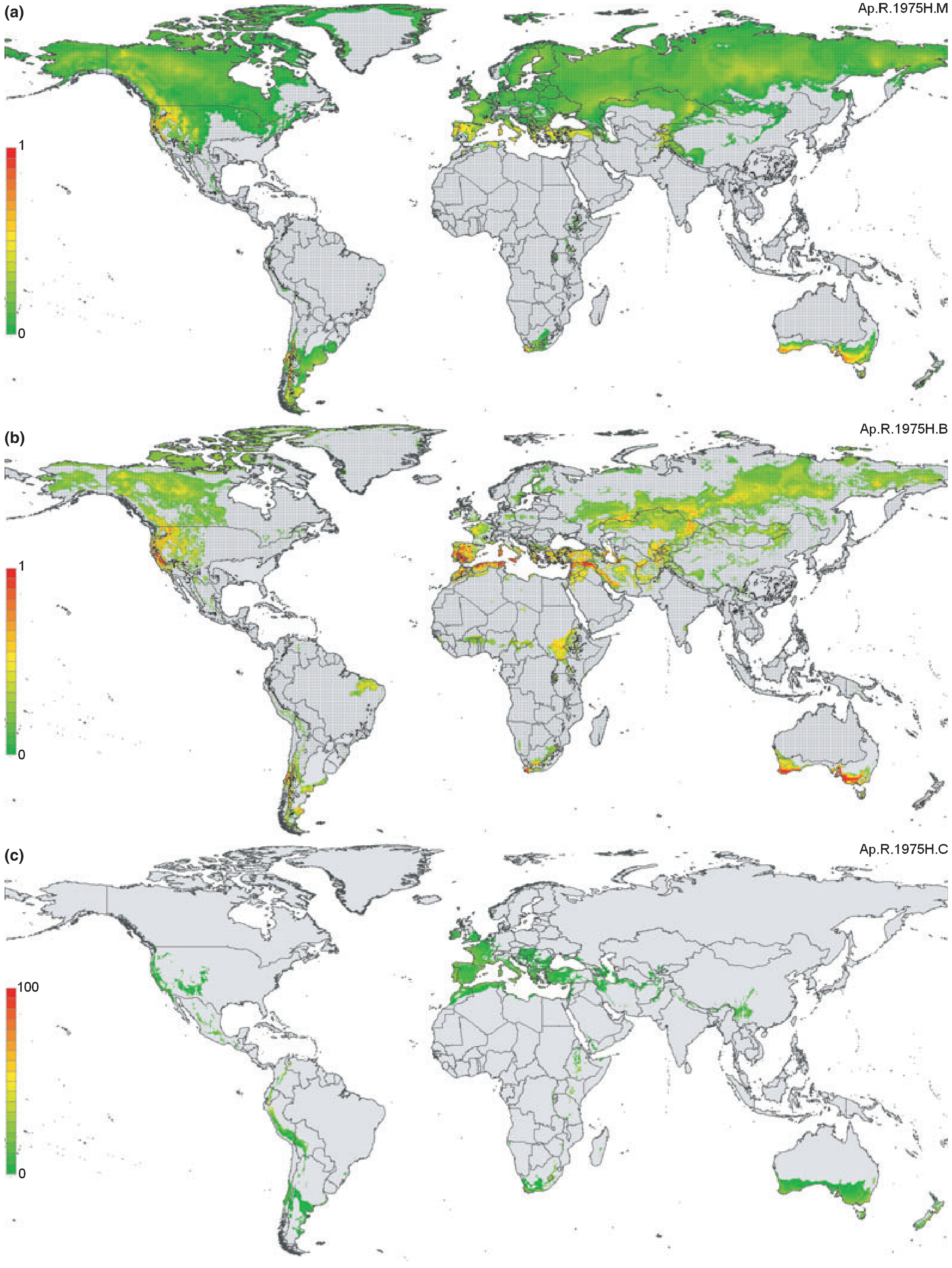


Figure 5 Model projections for the potential distribution of *Acacia pycnantha* (Ap) based on recent historical climates (1975H). Three models (MaxEnt, M; BRT, B; and CLIMEX, C) were applied to restricted (R) and full (F) training data sets. Symbology follows Fig. 4.

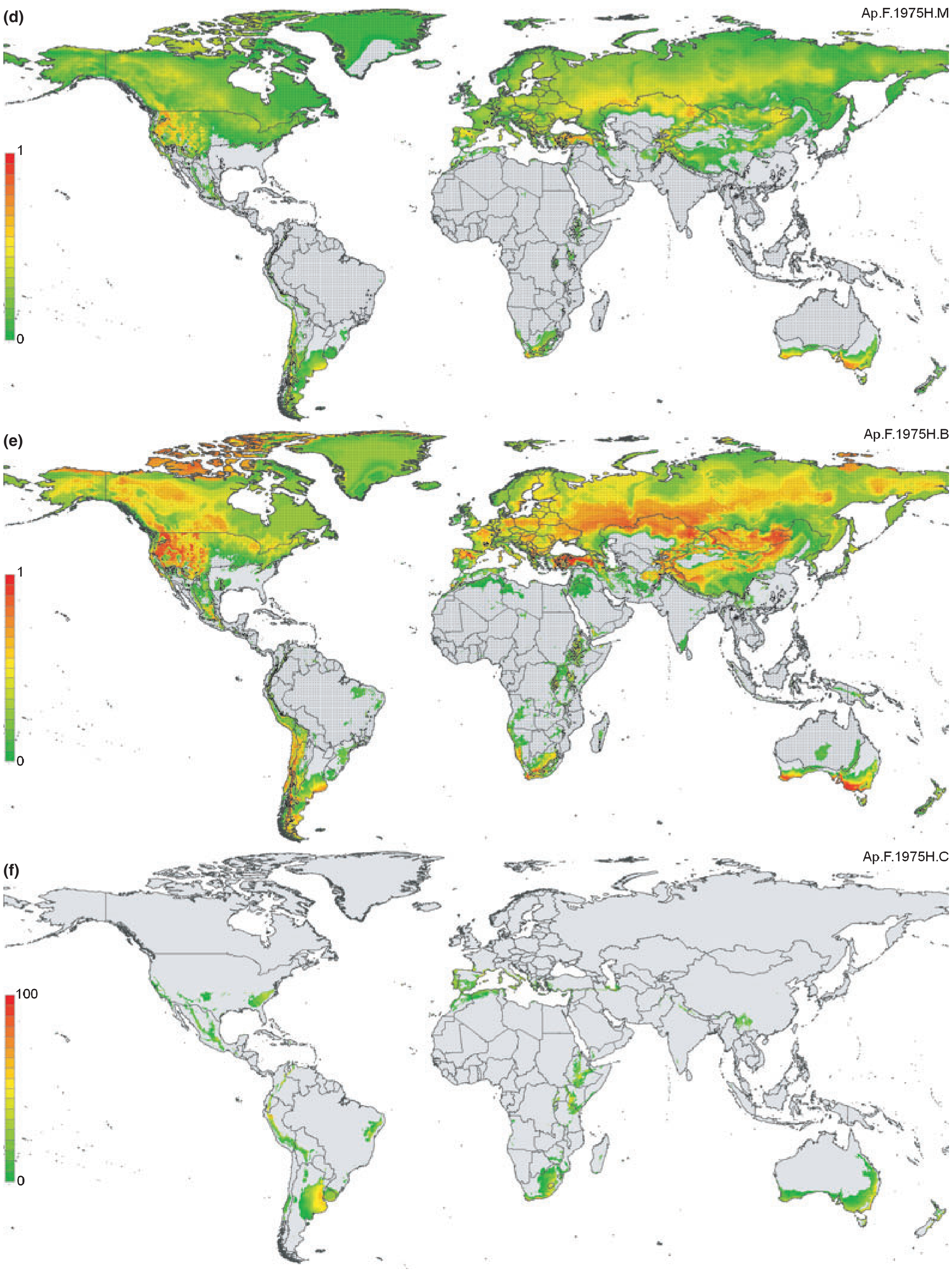


Figure 5 Continued.

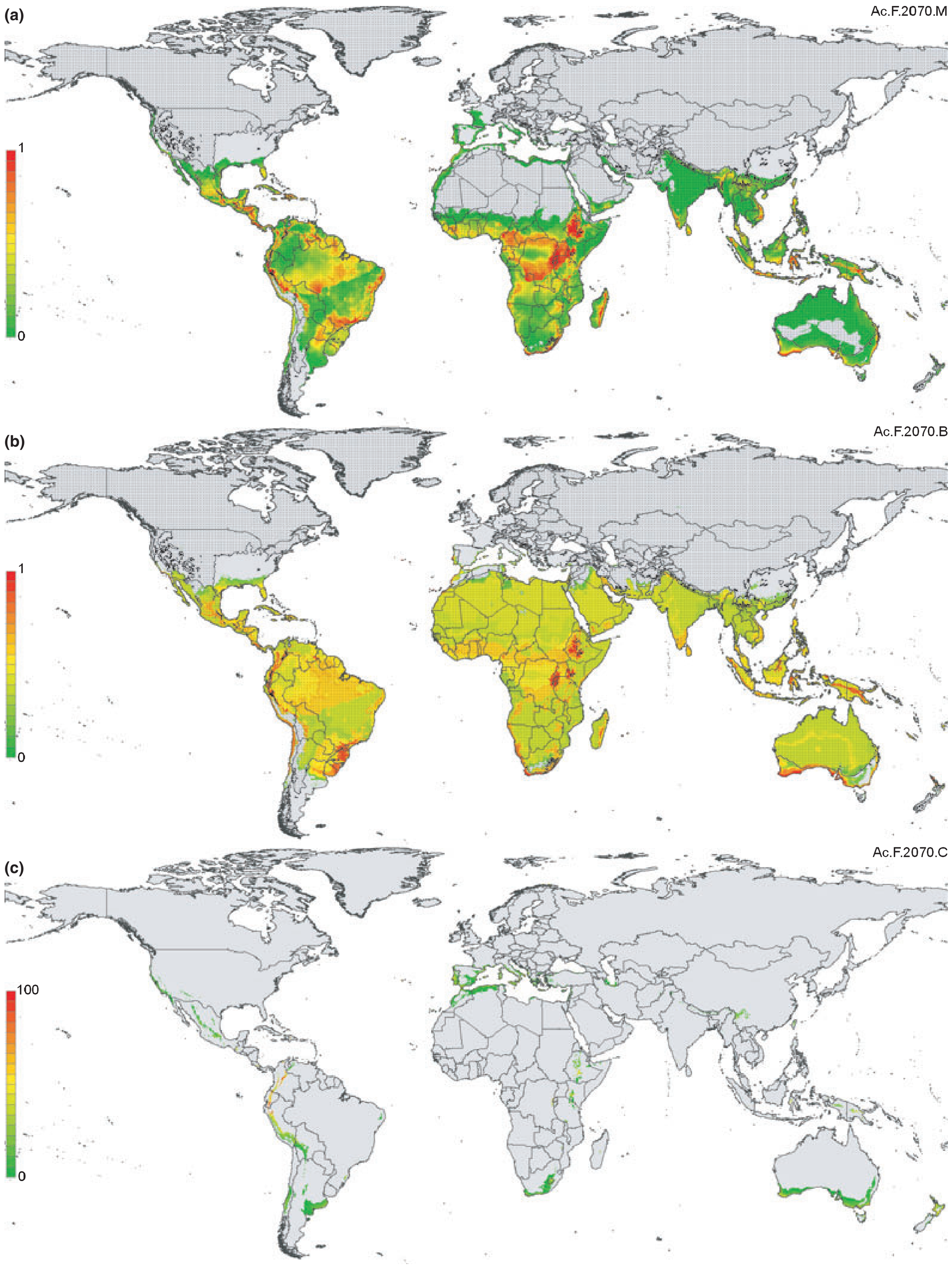


Figure 6 Model projections for the potential distribution of *Acacia cyclops* (Ac) based on future modelled climates (2070). Three models (MaxEnt, M; BRT, B; and CLIMEX, C) were applied to the full (F) training data set. Symbology follows Fig. 4.

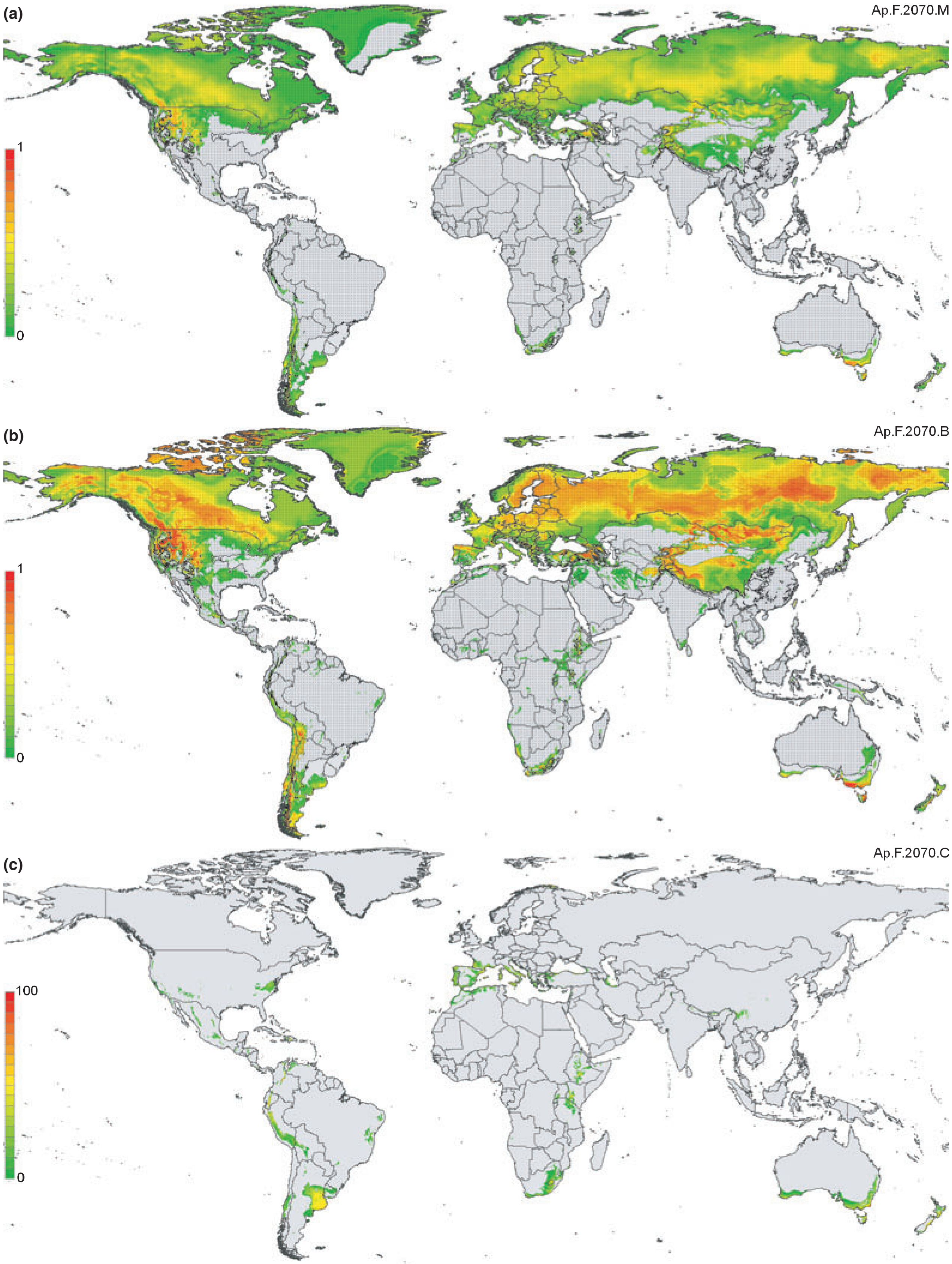


Figure 7 Model projections for the potential distribution of *Acacia pycnantha* (Ap) based on future modelled climates (2070). Three models (MAXENT, M; BRT, B and CLIMEX, C) were applied to the full (F) training data set. Symbology follows Fig. 4.

models. In regions such as South Africa and Australia that have hard (southern) continental boundaries, this polewards range shift leads to a contraction in the projected potential area (Figs 6, 7, S6 & S7).

DISCUSSION

The distribution patterns of Australian acacias provide a unique opportunity for investigating many practical and theoretical issues associated with bioclimatic modelling and its application to novel climates, such as invasive species and future climate change risk assessments. For example, *A. cyclops* and *A. pycnantha* both have elements of native-range expansion, alien invasions within their native continent, and broad-scale alien invasions in other continents. Our study found substantial variation in the projected range limits for *A. cyclops* and *A. pycnantha* among the three modelling techniques and between models fitted with restricted or full training data sets.

There are obviously many issues that this manuscript could discuss with respect to bioclimatic modelling, such as data quality and appropriate statistics for testing models. We have focussed our discussion on (1) the interpretation of model projections, (2) explaining differences between models and (3) how we might best proceed with modelling species ranges in novel climates.

Model interpretation

All models were statistically significant when tested against their training data, with independent South African data and globally, but there was considerable variation among modelling techniques and between models fitted with restricted or full training data sets in both their sensitivity and modelled prevalence. Generally, the extra information in full training data sets encompassed a broader environmental range and increased the sensitivity of the models. Gains were marginal for both species using MaxEnt, moderate for both species using BRT and substantial for *A. cyclops* and marginal for *A. pycnantha* using CLIMEX. It is likely that the CLIMEX projections based on the restricted data set, particularly for *A. cyclops*, were too conservative and therefore potentially underestimated suitable climate space as indicated by the low sensitivity value when projected to South Africa (Table 2). However, the method used to construct the restricted data set models goes against recommended practice for CLIMEX modelling because of the potential value in the data being withheld from the model (Kriticos & Randall, 2001; Sutherst & Bourne, 2009). As might be expected, the increases in the sensitivity of the models fitted with full training data sets were also accompanied by increases in model prevalence scores, as they included information from locations occupying more extreme climatic conditions than the native-range data set. Interestingly, this additional information had a different impact on the correlative and mechanistic models.

The CLIMEX modelling technique allows new distribution records or ecophysiological information to be included in the model by iterative adjustments to the restricted data set parameters, with a coincident change in the projection area to encompass ecoclimatically similar locations. For our acacia models, the prevalence of the CLIMEX models increased to encompass the points in the full data set with only moderate increases in model prevalence elsewhere confined to ecologically reasonable climates (compare Figs 4c & 4f). In contrast, the additional information included in the full training data set sometimes adversely affected the discriminative correlative models; increased sensitivity came at the expense of proportionally greater increases in modelled prevalence and consequently reduced the statistical significance of the models. Where the alien distribution data included locations outside of the climatic range spanned by the native distribution records, it also included additional areas of model background that were incompletely invaded (Fig. S1). Therefore, models trained on the complete data sets used a background sample that included areas of high climatic suitability that were occupied in the native range and unoccupied in the exotic range. This pattern of increasing confusion in correlative models trained on full vs. restricted range data is apparent in both the changes in the potential range boundaries and changes in the relative suitability patterns within the boundaries for the models (e.g. compare Fig. 4a with 4d, Fig. 4b with 4e). In both of these correlative model comparisons, the full data set models classified considerably less area as highly suitable, indicating that the model's ability to discriminate relative climate suitability was reduced. Moreover, the extra information in the full data sets did not necessarily result in closed Bioclim variable response curves, even when the variable range of the background was broad relative to that of the distribution points (Fig. S1). Taken together, our results indicate that combining native and alien distribution records in discriminative correlative models does not consistently improve model projections. If undertaken as a methodological choice, careful interpretation of the input data and the model results is imperative.

A significant advantage of testing the models in South Africa is that we were able to observe how the models performed against an independent set of high-quality data, where the ecological implications of prevalence and sensitivity can be interpreted with reasonable confidence. Of particular interest to invasion ecologists and biosecurity managers are regions of projected suitable climates that do not currently have distribution records. In South Africa, the correlative models projected areas of climatic suitability in interpolation (MESS+) space beyond the current distribution in the Eastern Cape, particularly for *A. cyclops* (Figs S4 & S5). In contrast, the CLIMEX model projected areas of climatic suitability in the central provinces west and north of Lesotho (Figs S4f & S5f). If these projections are plausible, the absence of these two acacias may be due to factors not included in the models. For example, regions north and west of Lesotho are known to have up to 60 nights of frost annually (Schulze, 1965), a range-limiting climate variable not captured well by climate averages (Zimmermann *et al.*, 2009). When assessed against high-quality data, models can be used to generate testable hypotheses to provide insight into the relative importance of climate, dispersal and biotic interactions on the present range limits of these species.

Irrespective of the model performance in South Africa, for invasive species risk assessments, bioclimatic models ideally need to be able to perform in a robust manner globally. It was clear from the mapped model results that model performance in South Africa was not representative of model performance globally, indicating performance in South Africa cannot be usefully generalized elsewhere. This study found substantial differences in the global projections of range limits for *A. cyclops* and *A. pycnantha* among the three bioclimatic models (Figs 4 & 5). Both MaxEnt and BRT models projected implausible areas of high suitability for *A. cyclops* in the tropics, subtropics and deserts and for *A. pycnantha* at very high latitudes in the Northern Hemisphere. In contrast, the CLIMEX model projections were more constrained and restricted to the native range and closely matched climates, incidentally more closely resembling the MESS+ regions from the correlative models.

Explaining model differences

The differences in projections between the correlative models and CLIMEX are influenced, in part, by the respective methods for fitting species ranges. MaxEnt and BRT models seek to discriminate between distribution records and the background using the entire presence data set to fit the response functions. In contrast, the CLIMEX model fitting process explicitly focuses attention on the peripheral distribution records and their relationship with adjacent, apparently climatically unsuitable regions. The CLIMEX user's challenge is to identify solutions that accord with knowledge across multiple domains. When a conflict is discovered between the information at hand and the model, all data and knowledge sources (distribution records, ecophysiological data, climate data, theoretical precepts and the relevance of model mechanisms) are scrutinized to identify plausible, parsimonious explanations. In this way, we were able to identify and actively exclude distribution record outliers that were found in apparently climatically implausible locations, but that were not detected in the Bioclim variable exploration used for the correlative models (Fig. S1).

A second influence on model performance is how the models handle extrapolation. In the global projections, it was clear that the MaxEnt and BRT models were extrapolating (MESS−) beyond their training data to project climatic suitability in parts of the world where it is implausible for large woody shrubs to grow (e.g. the Sahara desert and Greenland; Figs 4 & 5). MESS maps also made it very clear that regions of correlative model extrapolation dominated global projections in future climate scenarios (Figs 6, 7, S6 & S7). The three modelling techniques applied here differ considerably in how they deal with extrapolation (Fig. 8). MaxEnt provides the user with four options to control response curves: 'no extrapolation', 'clamping' (maintaining the suitability value at the limits of the training data), 'don't clamp' (continuing the trajectory of the response curve at the limits of the training data) and 'fade by clamping' (reducing the suitability value by the difference between clamped and don't clamped output; Fig. 8a). BRT models produce the equivalent of clamping in MaxEnt (Fig. 8b). In this study, MaxEnt models used the clamping option, meaning that open-ended response functions often maintained high suitability values throughout the extrapolation space (Figs S2 & S3). These factors account for much of the implausible model projections clearly evident at the global scale. CLIMEX models, on the other hand, are fitted over the entire environmental domain (Fig. 8c). Parameters that contribute to the growth index (GI) consist of closed

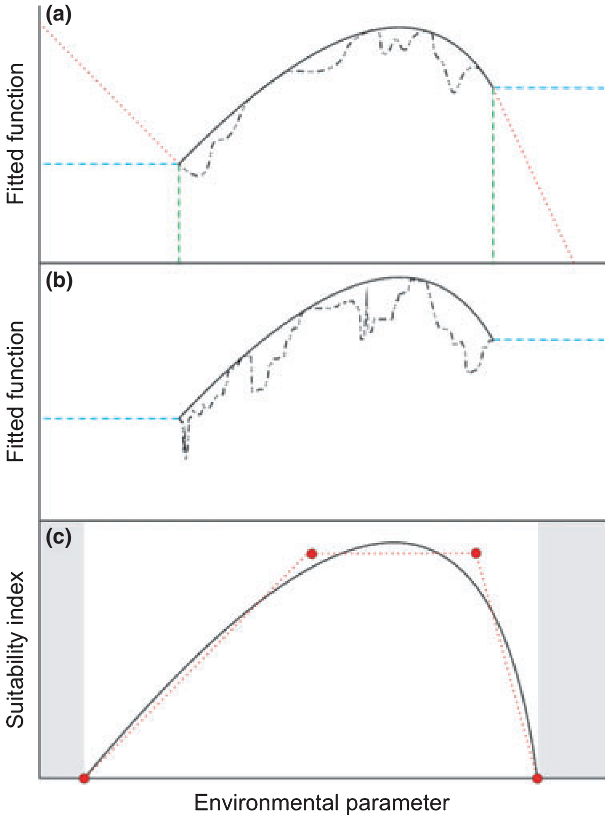


Figure 8 Hypothetical response curves used by MaxEnt, Boosted Regression Trees (BRT) and CLIMEX bioclimatic models. For the correlative models, the modelled ecological response curve (dash-dot lines) represents a reduced space relative to the physiological response curve (solid lines; *sensu* Austin, 1980) that is more closely approximated by CLIMEX. In extrapolation space, MaxEnt (a) has four options: 'don't extrapolate' (dark blue dashed lines), 'clamp' (light green dashed lines), 'don't clamp' (dotted red lines) and 'fade by clamping' (not illustrated, which reduces values by the difference between clamped and non-clamped output). BRT models (b) consistently 'clamp' projections in extrapolation space (dashed blue lines). CLIMEX models (c) have closed response curves (red dotted lines) based on four defined values (minimum, optima, maximum; red circles) and use stress functions (grey shading) to further constrain the range boundaries beyond the curve minima and maxima.

curves that are used by the model in a different way to correlative models (Sutherst *et al.*, 2007). CLIMEX also uses stress functions to further define unsuitable climate space. Stress functions largely define the species range, whereas the annual growth index (GI_A) and stresses indices, in combination, define the climate suitability (EI) within that range. Critically, these stress functions have the property of explicitly penalizing conditions that are more extreme than those which are inferred by the model to be unsuitable.

Improving bioclimatic models for novel climates

If we are to properly understand species invasions and the effects of anthropogenic climate change, we need to be confident that our models are capturing key determinants of the fundamental niche and that projections beyond the training regions are meaningful and reliable. Our study is not the first to describe differences among models in the limits to species distributions (Pearson *et al.*, 2006; Elith & Graham, 2009) or to highlight the problems with using correlative bioclimatic models for extrapolation (e.g. Hirzel & Le Lay, 2008; Sutherst & Bourne, 2009). Although important advances have been made in tools that facilitate careful interpretation of model outputs (Elith *et al.*, 2010, 2011), there are still avenues for research and development that could improve the ability of bioclimatic models to handle novel climates. Based on our experience, we suggest four areas of endeavour: (1) defining the background for training the MaxEnt models and the background or sampling area for pseudo-absence points in the BRT models, (2) adding an ability to create more ecologically realistic response functions, (3) developing more relevant variables for bioclimatic modelling and (4) further integrating mechanistic and correlative model techniques.

The choice of the background (MaxEnt and BRT) or sampling area for the generation of pseudo-absences (BRT) remains a matter of judgement and involves many considerations (Elith *et al.*, 2010). If the background is either too narrowly or too broadly defined, it can compromise model performance (VanDerWal *et al.*, 2009) and its ability to accurately capture or project distributions. For example, increasing the size of the background will increase the background climate span relative to the climatic span of the distribution records and reduce the area where models are extrapolating. However, the reduced area of extrapolation comes at the expense of discriminating suitable environments at local scales, and places misleading emphasis on a reduced set of variables less relevant to the species being modelled (VanDerWal *et al.*, 2009; Elith *et al.*, 2010). There are no hard and fast rules for defining backgrounds, yet avoiding extrapolation using the whole world as a background would be clearly inappropriate. Our study is among the first to consider bioclimatic rules for defining the background (applying the Köppen–Geiger climate zones), and we demonstrate new tools for visualizing extrapolation space (MESS− overlays) and the interplay between the climate space spanned by the distribution records and the model training domains (Figs S1–S3). We chose to use Köppen–Geiger zones because of their strong climatic basis but, even so, we found that there was substantial variation among the bioclimatic variables in the ranges and frequency distributions spanned by the distribution records relative to the training domain (Fig. S1). Our choice of background deliberately avoided the inclusion of climates well outside of the range spanned by the distribution records. However, the training data may have had a truncated environmental domain because of species ranges abutting continental boundaries (Figs 1 & 2), and the models fitted open-ended response functions (Figs S2 & S3), leading to inappropriate modelled suitability in MESS− areas. Clearly, more thought needs to be given to defining the background in terms of how geographic space translates to climate space.

Both our study and others show that extrapolation needs to be treated with caution in correlative models (e.g. Kriticos & Randall, 2001; Sutherst & Bourne, 2009; Elith *et al.*, 2010). Many of the problems arise because of open-ended response curves. Extrapolating into novel climates with open-ended response curves in discriminatory correlative models can give biologically unrealistic projections when the response functions of particular variables are dominating model behaviour. One solution may be to incorporate options that determine response function behaviour in an ecologically meaningful way. Possibly of greater importance for the models of invasive species is the greater likelihood that in selecting models with high specificity, the model becomes over-fitted. Any methods that control response function behaviour should be ecophysiologically based (Austin, 1987; Austin & Meyers, 1996).

A further area for research would be to develop more relevant bioclimatic variables. The 35 Bioclim variables available in the CliMond data set (Kriticos *et al.*, 2011) are an expansion on the 19 core variables used for many models up to this point. However, new variables could be developed that more closely match critical stress mechanisms for organisms, such as frost or drought. Alternatively, variables could be developed based on extreme values rather than means (Zimmermann *et al.*, 2009), especially given that most projections of future climates indicate that the frequencies of events currently considered extreme will increase (Frei *et al.*, 2006).

The performance of the full data set CLIMEX models in this study highlights its utility for invasive species risk assessment and climate change studies. Outside of specific ecophysiological studies to populate parameters (e.g. Scott & Yeoh, 1999), the time and skill required to fit these models is similar to that of well-constructed correlative models. Nonetheless, efforts to improve the ability of CLIMEX models to be machine-fitted should continue while retaining one of the model's strengths, namely its ability to confront the user with conflicting evidence of habitat suitability and provide many of the means to resolve conflicts. The tools developed by Elith *et al.* (2010, 2011) allow for a better understanding of correlative model behaviour, insightful model critique and improved transparency. This research group is also exploring methods to incorporate non-climatic physiological layers into correlative models and move beyond climate-matching the realized species niche. The approach taken in this study highlights parallels between correlative modelling and the established methods of mechanistic models such as CLIMEX, and we recommend further exploration of the different insights they can provide.

CONCLUSIONS

Modelling species distributions, particularly potential distributions in novel climates, is fraught with numerous difficulties that can make projections highly uncertain. The combined threat of climate change and invasive species to biodiversity and production systems makes the development of robust approaches to modelling invasive species all the more important from a management perspective (Walther *et al.*, 2009). The use of new diagnostic tools for interpreting correlative model projections (Elith *et al.*, 2010), together with an understanding of the response functions, enabled us to have a much greater understanding of the strengths and limitations of the methods used. Our work illustrates the need for a cautious approach when projecting models into novel climates, for results that are consistent with all available information on the species and for ecologically relevant model components (e.g. response curves) that are open to scrutiny and critique (Venette *et al.*, 2010). In a practical sense, our findings also indicate that managing the spread and impacts of both invasive *Acacia* species appears justified in current climates and will remain a priority under projected climate change scenarios. These findings are important not only for directing control efforts of these invasive species in their alien ranges in Australia and elsewhere but also for guiding the appropriate management of range shifts for native populations of *A. cyclops* and *A. pycnantha*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Species distribution data processing for South Africa.

Appendix S2 Supporting information for physiological parameters used in the CLIMEX models.

Figure S1 Bioclim variable box and whisker plots.

Figure S2 Bioclimatic parameter response curves for *Acacia cyclops*.

Figure S3 Bioclimatic parameter response curves for *Acacia pycnantha*.

Figure S4 Recent historical projections for *Acacia cyclops* in South Africa.

Figure S5 Recent historical projections for *Acacia pycnantha* in South Africa.

Figure S6 Future (2070) global projections for *Acacia cyclops* modelled with the restricted dataset.

Figure S7 Future (2070) global projections for *Acacia pycnantha* modelled with the restricted dataset.

Figure S8 Spatial distribution of limiting factors for MaxEnt modelling.

Table S1 Physiological parameters used in the CLIMEX models.

BIOSKETCH

This project is part of a multi-institution collaboration between Australian and South African scientists using native and alien range studies to explore exchanged invasive plants.

Bruce Webber is a plant ecophysiologist with research interests in plant resource allocation and plant–animal interactions. He currently works with the CSIRO Climate Adaptation Flagship to apply these interests to understanding the dynamics of plant invasions within the context of a rapidly changing climate.

Author contributions: C.J.Y. and G.F.M. initiated the collaboration, G.F.M., C.J.Y., J.K.S., B.L.W. and D.C.LeM. conceived the research ideas, J.J.LeR. and N.O. contributed core data; A.McN., B.L.W., D.C.LeM. and C.J.Y. processed the distribution data, B.L.W., D.C.LeM., D.J.K., C.J.Y., J.K.S., and A.McN. ran the models, B.L.W., A.McN., D.J.K., N.O., D.C.LeM. and C.J.Y. analysed the model output, and B.L.W. led the writing.

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