

# Multi-species distribution modelling highlights the Adelaide Geosyncline, South Australia, as an important continental-scale arid-zone refugium

GREG R. GUERIN<sup>1</sup> AND ANDREW J. LOWE<sup>1,2\*</sup>

<sup>1</sup>*Australian Centre for Evolutionary Biology and Biodiversity, School of Earth and Environmental Science University of Adelaide, North Terrace, SA 5005, Australia (Email: andrew.lowe@adelaide.edu.au), and* <sup>2</sup>*Department of Environment and Natural Resources, Adelaide, South Australia, Australia*

**Abstract** The mainland portion of the Adelaide Geosyncline (Mount Lofty and Flinders Ranges) has been postulated as an important arid-zone climate refugium for Australia. To test the sensitivity of this putative Australian arid biome refugium to contemporary climate change, we compared Generalized Additive Modelling and MaxEnt distribution models for 20 vascular plant species. We aimed to identify shared patterns to inform priority areas for management. Models based on current climate were projected onto a hypothetical 2050 climate with a 1.5°C increase in temperature and 8% decrease in rainfall. Individual comparisons and combined outputs of logistic models for all 20 species showed range contraction to shared refugia in the Flinders Ranges and southern Mount Lofty Ranges. Modelling suggests the Flinders Ranges will experience species turnover while suitable climatic habitat will be retained in the Mount Lofty Ranges for the current suite of species. Fragmentation of the southern Mount Lofty Ranges poses management challenges for conserving species diversity with warming and drying. Although projected models must be interpreted carefully, they suggest the region will remain an important but threatened refugium for mesic species at a continental scale.

**Key words:** bioclimatic distribution modelling, climate change, Flinders Ranges, fragmentation, Mount Lofty Ranges, refugia.

## INTRODUCTION

Arid Australia, covering most of the country's land surface area (rangeland vegetation communities cover 81% of the continent), has been understudied in terms of ecology and biogeography (Stafford-Smith & Morton 1990; Morton *et al.* 2011). Among the few semi-arid areas proposed as important past and future climatic refugia at a continental scale are the Mount Lofty and Flinders Ranges in South Australia (Byrne 2008; Byrne *et al.* 2008), because of topographical heterogeneity and climate. These ranges are an island of relatively mesic habitat isolated from similar habitat in south-eastern Australia (Armstrong *et al.* 2003).

The Mount Lofty and Flinders Ranges are, respectively, the southern and northern mainland sections of the Adelaide Geosyncline, an ancient marine sedimentary basin that was uplifted to form linear mountain ranges extending some 900 km from Kangaroo Island in the south to Arkaroola in the north (Preiss 2000). These regions have putatively acted as refugia during

Pleistocene climate oscillations and are refugia today for taxa that were more widespread during the Miocene (Byrne 2008; Byrne *et al.* 2008). The region therefore has continental biogeographical significance but its nature as a past, present and future refugium has not been formally tested.

Despite numerous studies globally, identification and testing of refugia in Australia has been limited (Byrne *et al.* 2008). Phylogeographic studies that have been conducted for Australia suggest a more complex pattern of refugia among species compared with the Northern Hemisphere. Byrne *et al.* (2008) speculated that the inland ranges were one of the few shared refugia in the Australian arid zone. While refugia in the Australian Wet Tropics have received attention (e.g. VanDerWal *et al.* 2009; Graham *et al.* 2010), there have been too few studies in southern and inland Australia to deduce patterns. The study described here is the first published work to examine the nature of a putative arid-zone refugium as proposed by Byrne (2008) and Byrne *et al.* (2008). Surprisingly few studies of Pleistocene or future refugia globally have compared multiple individual species to examine shared patterns.

\*Corresponding author.

Accepted for publication May 2012.

The Mount Lofty Ranges are a centre of species richness and endemism (Crisp *et al.* 2001) and one of 15 national biodiversity hotspots recognized by the Australian Government since 2003. Only 13% of pre-European (i.e. pre-1836) vegetation remains (Armstrong *et al.* 2003) and the remaining woodlands are fragmented. In addition to endemics, many plant species occurring in the ranges are at the western and/or northern extreme of their range and disjunct from populations of the same species in south-eastern Australia. The State Government of South Australia has implemented landscape-scale biodiversity corridors in the Mount Lofty and Flinders Ranges, the Cape Borda to Barossa and Flinders-Olary Nature-Links respectively (see <http://www.environment.sa.gov.au/naturelinks/index.html>). Testing of refugia and vulnerable habitats within these corridors will inform management priorities.

Mediterranean-climate ecosystems, such as those of the Adelaide Geosyncline region, have undergone degradation globally and climate change may compound the impacts of fragmentation (Abbott & Le Maitre 2010; Bardsley & Sweeney 2010; Lawson *et al.* 2010). Between 1950 and 2005, the average Australian surface temperature rose 0.95°C (Suppiah *et al.* 2006), with the southern and eastern regions more affected. A trend towards warmer, drier conditions is predicted for the Mount Lofty and Flinders Ranges under various SRES (Special Report on Emissions Scenarios, Intergovernmental Panel on Climate Change, 2001), carbon stabilization scenarios and climate models (Suppiah *et al.* 2006).

We examined the potential impacts of climate change on multiple species in the study region with a view to locating shared future refugia and identifying priority landscapes for management. We modelled bioclimatic distributions, projecting onto a hypothetical 2050 climate, which was the median of models and scenarios for 2030 and 2070. While such modelling has proved useful, the outputs need careful interpretation. Predictions of actual future distributions should consider not only suitable bioclimatic habitat but also demographics, ecological interactions, presence of native vegetation in bioclimatically suitable areas and landscape connectivity (Beaumont *et al.* 2005; Huntley *et al.* 2010; Penman *et al.* 2010; Scoble & Lowe 2010; Cochrane *et al.* 2011).

These considerations combined with bioclimatic modelling would provide a realistic assessment of adaptive capacity and ability to track geographically shifting habitat. Projected bioclimatic distributions are useful for predicting where habitat currently occupied could be located in the future, rather than the actual distribution at that time (Arif *et al.* 2007). Prediction of persistence requires data on how long species can survive unfavourable climate (Ashcroft 2010).

We modelled the bioclimatic distributions of 20 species with a range of distributions and habitat preferences. We compared individual species and combined model outputs. Aggregation of multiple models improves the ability to predict impacts on biodiversity within a region (Yates *et al.* 2010). We examined shared patterns among species with similar distributions and identified macrorefugia (see Ashcroft 2010) as key landscapes for management.

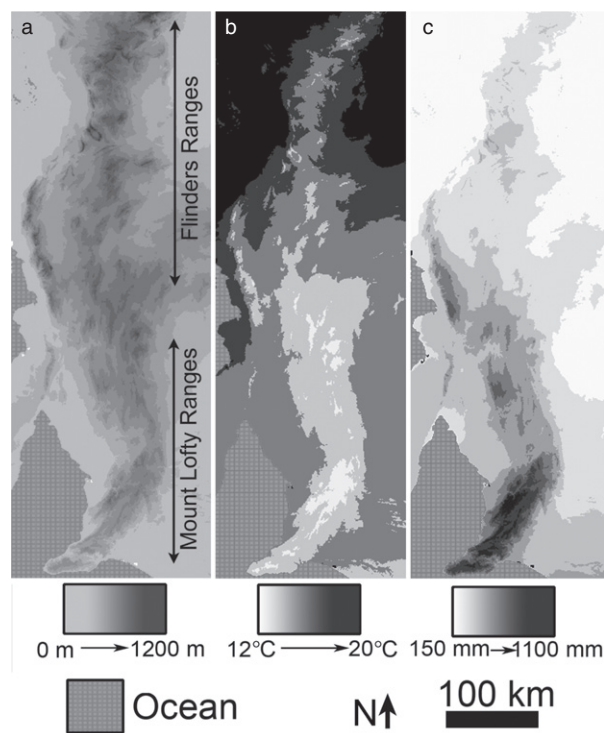
## METHODS

### Study area

Modelling encompassed a rectangular area enclosing the Adelaide Geosyncline region, South Australia (excluding Kangaroo Island), bound by 30°S, 137.8°E (north-west corner); 35.7°S, 139.65°E (south-east corner). The region is dominated by north-south orientated ranges (Mount Lofty Ranges (south); Flinders Ranges (north)) (Fig. 1a). The region has a Mediterranean climate with a mean temperature range of about 12–19°C (Fig. 1b) and mean annual rainfall range of about 150–1150 mm (Fig. 1c) (Hijmans *et al.* 2005a).

### Data sets and target species

WorldClim interpolated climate data (tile 410) with a resolution of 1 km<sup>2</sup> (Hijmans *et al.* 2005a) were imported into



**Fig. 1.** Mainland Adelaide Geosyncline locality and climate maps: (a) altitude; (b) mean temperature; (c) mean annual rainfall.

DIVA-GIS (version 7.1.6.2) (Hijmans *et al.* 2005b), to generate 19 bioclimatic variables (Table 1). These data are derived from Australian Bureau of Meteorology records to 2003.

Presence records (primarily herbarium) were sourced for 20 plant species (Table 2) from the Biological Databases of South Australia (Department for Environment and Natural Resources, accessed 20 August 2010). The spatial error of the

**Table 1.** Bioclimatic variables used for bioclimatic distribution modelling

Code	Bioclimatic variable	Used for modelling	Change applied for future climate scenario
Bio1	Annual mean temperature	N	–
Bio2	Mean diurnal temperature range (mean of monthly maximum temperature minus minimum temperature)	Y	None
Bio3	Isothermality (Bio2/Bio7*100)	N	–
Bio4	Temperature seasonality (standard deviation of monthly temperature*100)	N	–
Bio5	Maximum temperature of the warmest month	N	–
Bio6	Minimum temperature of the coldest month	Y	+1.5°C
Bio7	Temperature annual range (Bio5–Bio6)	N	–
Bio8	Mean temperature of wettest quarter	Y	+1.5°C
Bio9	Mean temperature of driest quarter	N	–
Bio10	Mean temperature of warmest quarter	N	–
Bio11	Mean temperature of coldest quarter	N	–
Bio12	Annual precipitation	Y	×0.92
Bio13	Precipitation of wettest month	N	–
Bio14	Precipitation of driest month	Y	×0.92
Bio15	Precipitation seasonality (coefficient of variation)	N	–
Bio16	Precipitation of wettest quarter	N	–
Bio17	Precipitation of driest quarter	N	–
Bio18	Precipitation of warmest quarter	Y	×0.92
Bio19	Precipitation of coldest quarter	N	–

**Table 2.** Taxa in the bioclimatic distribution modelling study and model evaluation statistics

Species	Distribution in region	Presence-only records	Presence records from P/A data set	MaxEnt mean AUC	GAM mean AUC
<i>Acacia pycnantha</i> Benth.	ML, SF, NF	690	735	0.90	0.80
<i>Acacia rivalis</i> J.M.Black	NF <sup>†</sup>	279	275	0.94	0.84
<i>Astroloma humifusum</i> (Cav.) R.Br.	ML, SF, NF	775	630	0.91	0.87
<i>Banksia marginata</i> Cav.	ML, SF	404	261	0.96	0.90
<i>Callitris glaucophylla</i> Joy Thomps. & L.A.S.Johnson	SF, NF	512	601	0.89	0.89
<i>Callitris gracilis</i> R.T.Baker	ML	216	81	0.90	0.80
<i>Calytrix tetragona</i> Labill.	ML, SF, NF	595	348	0.90	0.81
<i>Cassinia laevis</i> R.Br.	SF, NF	396	401	0.87	0.88
<i>Dianella revoluta</i> R.Br. var. <i>revoluta</i>	ML, SF, NF	376	241	0.88	0.83
<i>Dodonaea lobulata</i> F.Muell.	SF, NF	434	401	0.87	0.83
<i>Epacris impressa</i> Labill.	ML	303	316	0.98	0.93
<i>Exocarpos cupressiformis</i> Labill.	ML, SF	479	350	0.95	0.88
<i>Goodenia vernicosa</i> J.M.Black	NF <sup>†</sup>	96	73	0.93	0.75
<i>Hakea carinata</i> F.Muell. ex Meissner	ML, SF	413	280	0.96	0.85
<i>Hibbertia exutiaciens</i> N.A.Wakef.	ML, SF	419	530	0.96	0.88
<i>Platylobium obtusangulum</i> Hook.	ML	476	483	0.97	0.89
<i>Pultenaea daphnoides</i> Wendl.	ML	389	408	0.98	0.92
<i>Pultenaea largiflorens</i> F.Muell. ex Benth.	ML, SF, NF	395	287	0.95	0.85
<i>Tetratheca pilosa</i> Labill. ssp. <i>pilosa</i>	ML	436	366	0.97	0.92
<i>Xanthorrhoea quadrangulata</i> F.Muell.	ML, SF, NF <sup>†</sup>	232	257	0.91	0.83

Regions do not represent bioregions but descriptive geographic categories. <sup>†</sup>Endemic to the study region. AUC, area under Receiving Operator Characteristic; GAM, Generalized Additive Modelling; ML, Mount Lofty Ranges; NF, northern Flinders Ranges; SF, southern Flinders Ranges.

records varied but for the vast majority was well below 1 km and so acceptable for use with 1 km<sup>2</sup> resolution climate data. The less spatially accurate records were almost exclusively earlier collections. These were retained to represent a broader range of localities and habitats pre clearing of native vegetation. A presence/absence matrix was generated using presence data from 3567 systematic survey plots throughout the region using the 'simba' package in R (version 2.11.1) (Jurasinski & Retzer 2010; R Development Core Team 2010).

Bioclimatic data were extracted for presences and survey plots in DIVA-GIS. Records duplicated within grid cells were discarded.

Target species were selected to represent a range of distributions, habitats (including high altitude and lower slopes) and taxonomic groups. Distributions replicated by the study species include those largely restricted to the Mount Lofty Ranges (four species); Mount Lofty Ranges to southern Flinders Ranges (five species); Mount Lofty Ranges to northern Flinders Ranges (seven species, including one endemic species), southern Flinders Ranges to northern Flinders Ranges (two species) and endemic to the northern Flinders Ranges (two species).

Soils data were sourced for the study area (Soil and Land Program 2007). The available data are broad categorical soil types, which could not be used for modelling as relevant mapping has only been conducted for the southern agricultural areas of the study region. Geological data at a resolution considered meaningful in the context of the climate layers used and spatial scale of the study were not available. More importantly, geological units may provide misleading results if used as proxies for soils as drivers of species occurrence (see Discussion). Nevertheless, climate data alone are typically sufficient to predict distributions at this scale (Armstrong & Garnett 2011).

### Bioclimatic distribution modelling

Species typically have individual responses to environmental gradients and modelling probability of occurrence along gradients can test the relationship between species occurrences and environmental variables (Ysebaert *et al.* 2002; Keith 2009). Generalized Additive Modelling (GAM) is more flexible and better able to account for complex responses than Generalized Linear Modelling (GLM) (Yee & Mitchell 1991; Oksanen & Minchin 2002; Barry & Elith 2006). Generalized Additive Modelling uses presence/absence data, which typically outperform presence-only data sets in terms of model predictions (Barry & Elith 2006). Presence/absence models have the disadvantage of often lesser spatial and temporal distribution of available records but the advantage of systematically recorded absences (Barry & Elith 2006). Presence-only distribution modelling takes advantage principally of herbarium records that provide a wider spatial and temporal coverage than presence/absence (plot-based) records (Beaumont *et al.* 2005; Elith *et al.* 2006; Tsoar *et al.* 2007).

Principal components analysis (PCA) was conducted on the 19 bioclimatic variables for sites in the presence/absence data set to assist in the selection of a reduced number of variables that accounted for the variation in

climate among sites and were not strongly inter-correlated. PCA was conducted using standardized variables and varimax rotation in Ginkgo (Bouxin 2005; De Caceres *et al.* 2007) and R.

Two modelling approaches were used: MaxEnt (presence-only data set) and GAM (presence/absence data set). MaxEnt generates probability distributions with 'maximum entropy' (most spread out), subject to the constraints of environmental variables where a species has been recorded (Phillips *et al.* 2006). MaxEnt models were generated in Maximum Entropy Species Distribution Modelling Software (version 3.3.3a) (Phillips *et al.* 2006).

Logistic GAM is a form of GLM that fits a series of spline functions predicting likelihood of occurrence along predictor environmental axes (Barry & Elith 2006). Generalized Additive Modelling distribution models using selected bioclimatic variables and outputting distribution maps were generated in R using the functions of packages 'gam', 'raster', 'ade4', 'rJava', 'dismo' and 'SDMTools' (Dray & Dufour 2007; Bivand *et al.* 2008; Urbanek 2010; VanDerWal *et al.* 2010; Hastie 2011; Hijmans *et al.* 2011; Hijmans & van Etten 2011) and DIVA-GIS.

Future climate scenarios were assessed using the online OzClim tool (<http://www.csiro.au/ozclim/home.do>) in conjunction with Suppiah *et al.* (2006). Models were projected onto a hypothetical future climate with a mean temperature increase of 1.5°C and a mean annual precipitation decrease of 8% (approach similar to Penman *et al.* 2010). The changed climate was chosen by taking the median values for change predicted by various climate change scenarios and models and between 2030 and 2070 predictions, to give an estimate for 2050.

For MaxEnt, five cross-validation replicates were performed for each species and the outputs averaged. For GAM, 75% of the data matrix was used to train models and 25% to test. The train/test data split was performed randomly five times and the outputs were averaged. All six bioclimatic covariates were initially included in GAM models. When required, non-statistically significant (i.e.  $P$ -values  $\geq 0.05$ ) covariates were sequentially removed and the models re-run until all included covariates were statistically significant.

The fit of models to the test data was evaluated using the test data sets by calculating the area under Receiving Operator Characteristic, or AUC (Ben-David 2008). We acknowledge there has been some debate as to the reliability of AUC values in assessing fit (Lobo *et al.* 2008; Synes & Osborne 2011).

### Regional evaluation and identification of key landscapes

It was clear from model outputs for individual species that there were very similar patterns emerging among species with similar distributions. Given these patterns, we concluded that a sound means of combining model outputs to better examine and communicate shared regional patterns was to overlay logistic maps for individual species and climate scenarios and average corresponding grid cells. While average suitability could confound high suitability for one species with low suitability for many species, combining maps for 20



species tends to iron out idiosyncrasies of individual species. High suitability for only one species within a grid cell is balanced by low suitability for the remainder so that the average is low. Maps were combined separately for MaxEnt and GAM as the outputs are inherently different. We combined outputs in conjunction with comparisons of individual species.

The difference between suitability values for corresponding grid cells in the resulting current and future climate scenario grids was calculated, so that grid cells represented the absolute change in suitability. We assessed patterns of change in suitable habitat and used the output grids to identify landscapes where suitable habitat was retained for multiple species. Output grids were overlaid with a GIS layer of the presence/absence of pre-European native vegetation maintained by the South Australian Department of Environment and Natural Resources to determine whether identified putative refugia were fragmented.

## RESULTS

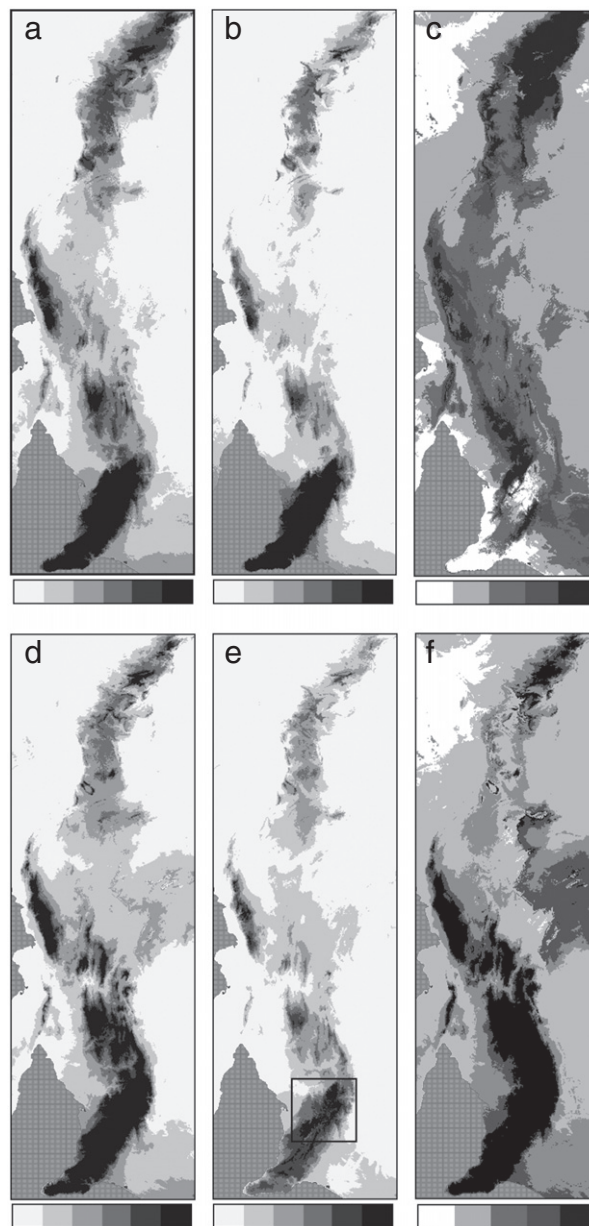
### Bioclimatic distribution modelling

A correlation biplot was generated from the PCA of bioclimatic variables using the first two axes, which explained 76% of the variance. Six bioclimatic variables were selected for use in distribution modelling that had the longest vectors and accounted for the distribution of vectors across the ordination space (to minimize correlation of variables) and were considered ecologically relevant (Table 1). Eighty distribution models with 1-km<sup>2</sup> pixel resolution were produced (20 taxa; current and future climate scenarios; MaxEnt and GAM). The AUCs of all but one individual GAM model (0.75) were more than 0.8 (Table 2).

### Regional evaluation and identification of key landscapes

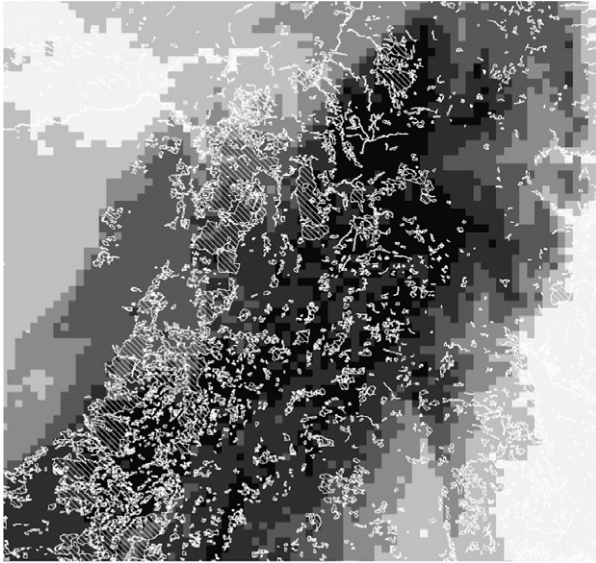
In response to the future climate scenario, MaxEnt projected suitability to decline sharply in areas such as the lower slopes of the Mount Lofty Ranges, lower slopes of the northern Flinders Ranges and the far northern Flinders Ranges (Fig. 2). This resulted in suitable habitat contracting away from these areas. Suitability declined little or increased slightly in the southern Mount Lofty Ranges (excluding lower slopes). Decline was also minimal in the northern Flinders Ranges between Wilpena and Gammon Ranges. Mean logistic scores for MaxEnt decreased from 0.078 to 0.051.

Generalized Additive Modelling projected suitability to decline throughout the region wherever it was initially high (Fig. 2). Suitable habitat was retained in localized high altitude areas such as the Gammon



**Fig. 2.** Combined habitat suitability maps for current and hypothetical 2050 climate for 20 study taxa. (a) MaxEnt, current climate; (b) MaxEnt, future climate; (c) MaxEnt, difference in logistic suitability values; (d) Generalized Additive Modelling (GAM), current climate; (e) GAM, future climate; (f) GAM, difference in logistic suitability values. Halftone legend divisions represent: (a–b) 0.05/(d–e) 0.025 increments of logistic values or (c) 0.025/(f) 0.0125 increments of suitability loss (halftone) or increase (white). Box in (e) highlights area shown in Figure 3.

Plateau (northern Flinders Ranges) and Mount Remarkable Range (southern Flinders Ranges). A large area of suitable habitat was retained in the southern Mount Lofty Ranges. Retained suitable areas were characterized by high initial suitability more so than



**Fig. 3.** Area highlighted by box on Figure 2e overlaid with remnant vegetation layer (white hatched polygons). Darker area is a putative refugium for near-future climate change (remaining high suitability in Generalized Additive Modelling models, slight increase in suitability in MaxEnt models). It contains some significant blocks of native vegetation but is highly fragmented. Scale: 70 km across figure.

low decline. However, an area with retained suitability and low decline was evident in the northern Flinders Ranges between Wilpena and Gammon Ranges. Mean logistic scores for GAM decreased from 0.042 to 0.024.

Shared patterns between individual species with similar characteristics were evident. Northern ranges of widespread species tended to decline in suitability resulting in contraction to more suitable southern areas. Suitable habitat for species restricted to northern areas tended to contract to higher altitude. Suitable habitat for southern species changed little or contracted to higher altitude.

Putative refugia were identified as follows: the southern Mount Lofty Ranges, where there was little change from high suitability in MaxEnt models and retained suitability despite decline in GAM models; and the northern Flinders Ranges between Wilpena and Gammon Ranges, where initial suitability was retained in both models albeit with shifts in suitability between species.

Superimposition of model outputs with the remnant native vegetation layer indicated that much of the predicted refugial area in the southern Mount Lofty Ranges coincides with heavily fragmented vegetation (Fig. 3). The predicted refugial area in the northern Flinders Ranges is not fragmented.

## DISCUSSION

### Predicted distribution shifts

Bioclimatic distribution modelling of 20 species replicating a range of current distributions and habitats, demonstrated that the topographic heterogeneity of the Adelaide Geosyncline region enabled suitable bioclimatic habitat to persist via range contraction rather than southerly shifts. There were consistent patterns despite some variation between models and species. The overall trend with warming and drying of climate was a decline in suitable habitat. Northern species, and northern populations of widespread species, were more affected. Habitat for widespread species tended to contract to the southern part of their range while habitat for more northern species contracted to higher altitude.

Combined distribution maps of multiple species also showed contraction of suitable habitat. The southern Mount Lofty Ranges, the wettest, coolest part of the region, was the most stable in terms of shared suitability with MaxEnt models and retained suitable habitat in GAM models despite decline, because of high initial suitability.

### Identification of shared refugia

Potential refugia were identified in the northern Flinders Ranges between Wilpena and Gammon Ranges and in the southern Mount Lofty Ranges. These areas had high initial suitability and underwent less decline or, in the case of GAM models for the southern Mount Lofty Ranges, retained significant suitable habitat despite decline. Habitat for most species in the south was retained (if reduced), whereas in the northern Flinders Ranges, higher altitude habitats became unsuitable for species currently restricted to them while becoming more suitable for species currently occurring at lower altitudes. This suggests northern refugial areas may be important for climate change adaptation while undergoing species turnover. The modelling suggests species that may disappear from restricted higher altitude habitats in the Flinders Ranges will persist within the southern parts of their current ranges.

Bioclimatic ranges contracted, rather than shifting to currently unoccupied ground. This fits with Byrne's (2008) conclusion that late Pleistocene climatic oscillations in southern Australia triggered localized refugia rather than geographical shifts. The scale of our analysis means our models cannot test individual localized microrefugia for these taxa but the pattern of contraction to shared refugia directly supports Byrne *et al.*'s

(2008) suspicion that inland ranges, especially at the periphery of the interior Australian arid zone, are important shared refugia.

### Assessment of the approach

Soils data of sufficient spatial coverage to be useful for this study are not available. While maps depicting regional surface geology units as polygons are available, these data are likely to be a relatively poor proxy for soil types without correlates for other historical and contemporary factors that influence soil formation including climate, erosion and deposition, age of land surface and biota (McKenzie & Ryan 1999).

Regionally, soils over the Adelaide Geosyncline geological unit consist of shallow to moderately deep duplexes on lower slopes and low sloping ( $\pm$  elevated) plains with shallow loams, clays and earths on rocky rises (Australian Natural Resource Atlas (<http://www.anra.gov.au/>, accessed May 2012)). Deep lateritic soils occur on the Fleurieu Peninsula and shallow sandy soils occur in localized areas. Floodplains are limited in extent and characterized by clays and clay loams.

While some species in the region may be more prevalent on particular soils, this tends to generate patchiness within a broad climate niche. Even more importantly, most of the species used in this study occur on multiple sandy, loamy, clayey or rocky soil types. For some species, soils may further restrict potential distribution within the modelled area of suitable climatic habitat and this would limit the application of this study at a local scale.

Distribution modelling using coarse climate grids interpolated from regional weather stations is only able to infer macrorefugia (Ashcroft 2010). Even where regional climate becomes unfavourable, microrefugia may allow species to persist locally, but microclimates cannot be accurately inferred from interpolated data.

Climate change may be more complicated than our projected 2050 climate (Suppiah *et al.* 2006). Also, some impacts of climate change may not be reflected in mean climate, for example, the impact on extreme weather and fire regimes (Suppiah *et al.* 2006). Nevertheless, the scenario used here gives an indication of trends that can be expected at a regional scale. Climate is changing now and species may already be experiencing shifts in suitable habitat.

Bioclimatic distribution models have limitations when considered in isolation and used to predict future distributions rather than the area of suitable habitat. They assume species are unable to adapt or occupy other bioclimatic habitat and they assume uniform bioclimatic tolerances among populations, or unimpeded dispersal and/or gene flow (Keith *et al.* 2008; Graham *et al.* 2010; Scoble & Lowe 2010).

Bioclimatic models under changed climate suggest where bioclimatic habitat occupied by species today may lie in the future, but cannot predict future distributions without genetic data, particularly. Such synthesis could assess barriers to gene flow and adaptive capacity. Additionally, the physiological tolerances of these species are not known.

The use of multiple species and replication of distribution patterns resulted in reasonably consistent predictions under climate change at a regional level. This suggests our results can be extrapolated to a

**Table 3.** Key landscapes and management implications based on changes in suitable habitat for 20 species in the mainland Adelaide Geosyncline region

Landscape	Predicted change and key attributes	Management implication
Southern Mount Lofty Ranges	Significant area of suitable habitat retained. Remnant native vegetation is fragmented.	This area is identified as a refugium that will be buffered to some extent from the impacts of climate change in terms of species distributions relative to other areas. Given the intersection of a fragmented landscape with a climatic refugium, restoration is a priority in this area.
Northern Flinders Ranges (Wilpena to Gammon Ranges)	Retained shared suitability but changes in which species habitat suitable for. Potentially important refugium for northern Flinders Ranges endemics. Native vegetation is not fragmented but grazing plus invasive species may impact condition.	This area is identified as a refugium. Suitable habitat here for species with broad latitudinal distributions in the region is predicted to become increasingly restricted and species turnover is expected. Active management is required to maintain habitat quality and connectivity. Examples of issues for management are fire regimes, grazing by livestock and feral goats, weed management, quality and connectivity of surrounding habitats.
Entire region	Change is uncertain and adaptive management is required.	To test model predictions and inform adaptive management, long-term systematic monitoring is recommended in key landscapes.



wider range of species with similar distribution characteristics, notwithstanding the above qualifications. Decline in the area of suitable habitat can be expected for a range of species, particularly in the Flinders Ranges, where a number of species appear to persist today close to the margins of their bioclimatic habitat. We did not test whether areas becoming less suitable will receive an influx of species from hotter, drier habitats on surrounding plains.

### Management implications

A potential climatic refugium was identified in the southern Mount Lofty Ranges. Suitable habitat was retained for the current suite of species, even when suitability for the same species declined in the north. This projected refugium intersects a fragmented landscape. A regional priority for conserving both widespread species and those restricted to this area is the management of remnant vegetation and restoration of cleared land. This could counteract the negative consequences of degradation due to landscape change and invasive species (Table 3).

A second major refugial area was identified in the northern Flinders Ranges. This landscape is relatively unfragmented but would benefit from management that promotes habitat quality and connectivity to enable lowland species to contract to higher altitudes and give restricted ridgetop species better chances of survival. Habitat quality would benefit from appropriate management of invasive species (e.g. weeds, goats), grazing and fire regimes.

### ACKNOWLEDGEMENTS

We thank the South Australian Premier's Science and Research Fund, Terrestrial Ecosystems Research Network, Australian Research Council (LP110100721), Michael Stead and the South Australia Department of Environment and Natural Resources, Sonia Croft and Jan Rowland for provision of data from the Biological Database of South Australia and soil mapping.

### REFERENCES

- Abbott I. & Le Maitre D. (2010) Monitoring the impact of climate change on biodiversity: the challenge of megadiverse Mediterranean climate ecosystems. *Austral Ecol.* **35**, 406–22.
- Arif S., Adams D. C. & Wicknick J. A. (2007) Bioclimatic modelling, morphology, and behaviour reveal alternative mechanisms regulating the distributions of two parapatric salamander species. *Evol. Ecol. Res.* **9**, 843–54.
- Armstrong D. M., Croft S. J. & Foulkes J. N. (2003) *A Biological Survey of the Southern Mount Lofty Ranges, South Australia, 2000–2001*. Department for Environment and Heritage, South Australia.
- Armstrong G. & Garnett S. T. (2011) Landscape partitioning among *Triodia* spp. (Poaceae) in the fire prone Kimberley, north-west Australia. *Austral Ecol.* **36**, 849–57.
- Ashcroft M. B. (2010) Identifying refugia from climate change. *J. Biogeogr.* **37**, 1407–13.
- Bardsley D. K. & Sweeney S. M. (2010) Guiding climate change adaptation within vulnerable natural resource management systems. *Environ. Manage.* **45**, 1127–41.
- Barry S. & Elith J. E. (2006) Error and uncertainty in habitat models. *J. Appl. Ecol.* **43**, 413–23.
- Beaumont L. J., Hughes L. & Poulsen M. (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecol. Modell.* **186**, 250–69.
- Ben-David A. (2008) About the relationship between ROC curves and Cohen's kappa. *Eng. Appl. Artif. Intell.* **21**, 874–82.
- Bivand R. S., Pebesma E. J. & Gomez-Rubio V. (2008) *Applied Spatial Data Analysis with R*. Springer, New York.
- Bouxin G. (2005) Ginkgo, a multivariate analysis package. *J. Veg. Sci.* **16**, 355–9.
- Byrne M. (2008) Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography. *Quaternary Sci. Rev.* **27**, 2576–85.
- Byrne M., Yeates D. K., Joseph L. *et al.* (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Mol. Ecol.* **17**, 4398–417.
- Cochrane A., Daws M. I. & Hay F. R. (2011) Seed-based approach for identifying flora at risk from climate warming. *Austral Ecol.* **36**, 923–35.
- Crisp M. D., Laffan S., Linder H. P. & Monro A. (2001) Endemism in the Australian flora. *J. Biogeogr.* **28**, 183–98.
- De Caceres M., Oliva F., Font X. & Vives S. (2007) Ginkgo, a program for non-standard multivariate fuzzy analysis. *Adv. Fuzzy Sets Syst.* **2**, 41–56.
- Dray S. & Dufour A. B. (2007) The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Softw.* **22**, 1–20.
- Elith J., Graham C. H., Anderson R. P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–51.
- Graham C. H., VanDerWal J., Phillips S. J., Moritz C. & Williams S. E. (2010) Dynamic refugia and species persistence: tracking spatial shifts in habitat through time. *Ecography* **33**, 1062–9.
- Hastie T. (2011) gam: Generalized Additive Models. R package version 1.04 [Cited 1 April 2012.] Available from URL: <http://CRAN.R-project.org/package=gam>
- Hijmans R., Phillips S., Leathwick J. & Elith J. (2011) dismo: species distribution modeling. R package version 0.5-11 [Cited 1 April 2012.] Available from URL: <http://CRAN.R-project.org/package=dismo>
- Hijmans R. J., Cameron S. E., Parra J. L., Jones P. G. & Jarvis A. (2005a) Very high resolution interpolated climate surface for global land areas. *Int. J. Climatol.* **25**, 1965–78.
- Hijmans R. J., Guarino L., Jarvis A. *et al.* (2005b) DIVA-GIS, version 5. Manual [Cited 1 April 2012.] Available from URL: <http://www.diva-gis.org/>
- Hijmans R. J. & van Etten J. (2011) raster: geographic analysis and modeling with raster data. R package version 1.7-29 [Cited 1 April 2012.] Available from URL: <http://CRAN.R-project.org/package=raster>



- Huntley B., Barnard P., Altwegg R. *et al.* (2010) Beyond bioclimatic envelopes: dynamic species' range and abundance modelling in the context of climatic change. *Ecography* **33**, 621–6.
- Jurasinski G. & Retzer V. (2010) simba: a collection of functions for similarity analysis of vegetation data. R package version 0.3-2 [Cited 1 April 2012.] Available from URL: <http://CRAN.R-project.org/package=simba>
- Keith D. A. (2009) The interpretation, assessment and conservation of ecological communities. *Ecol. Manage. Restor.* **10**, S3–S15.
- Keith D. A., Akçakaya H. R., Thuiller W. *et al.* (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* **4**, 560–3.
- Lawson D. M., Regan H. M., Zedler P. H. & Franklin J. (2010) Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. *Glob. Change Biol.* **16**, 2518–29.
- Lobo J. M., Jiménez-Valverde A. & Real R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* **17**, 145–51.
- McKenzie N. J. & Ryan P. J. (1999) Spatial prediction of soil properties using environmental correlation. *Geoderma* **89**, 67–94.
- Morton S. R., Stafford Smith D. M., Dickman C. R. *et al.* (2011) A fresh framework for the ecology of arid Australia. *J. Arid Environ.* **75**, 313–29.
- Oksanen J. & Minchin P. R. (2002) Continuum theory revisited: what shape are species responses along ecological gradients? *Ecol. Modell.* **157**, 119–29.
- Penman T. D., Pike D. A., Webb J. K. & Shine R. (2010) Predicting the impact of climate change on Australia's most endangered snake, *Hoplocephalus bungaroides*. *Divers. Distrib.* **16**, 109–18.
- Phillips S. J., Anderson R. P. & Schapire R. E. (2006) Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**, 231–59.
- Preiss W. V. (2000) The Adelaide Geosyncline of South Australia and its significance in Neoproterozoic continental reconstruction. *Precambrian Res.* **100**, 21–63.
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0 [Cited 1 April 2012.] Available from URL: <http://www.R-project.org>
- Scoble J. & Lowe A. J. (2010) A case for incorporating phylogeography and landscape genetics into species distribution modelling approaches to improve climate adaptation and conservation planning. *Divers. Distrib.* **16**, 343–53.
- Soil and Land Program (2007) Land and Soil Spatial Data for Southern South Australia – GIS format [CD ROM]. Department of Water, Land and Biodiversity Conservation, South Australia.
- Stafford-Smith D. M. & Morton S. R. (1990) A framework for the ecology of arid Australia. *J. Arid Environ.* **18**, 255–78.
- Suppiah R., Preston B., Whetton P. H. *et al.* (2006) *Climate change under enhanced greenhouse conditions in South Australia. An updated report on: Assessment of climate change, impacts and risk management strategies relevant to South Australia.* Climate Impacts and Risk Group, CSIRO Marine and Atmospheric Research. June 2006 [Cited 1 April 2012.] Available from URL: [http://www.climatechange.sa.gov.au/uploads/pdf/SA\\_CMAR\\_report\\_High\\_resolution.pdf](http://www.climatechange.sa.gov.au/uploads/pdf/SA_CMAR_report_High_resolution.pdf)
- Synes N. W. & Osborne P. E. (2011) Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. *Glob. Ecol. Biogeogr.* **20**, 904–14.
- Tsoar A., Allouche O., Steinitz O., Rotem D. & Kadmon R. (2007) A comparative evaluation of presence-only methods for modelling species distribution. *Divers. Distrib.* **13**, 397–405.
- Urbanek S. (2010) rJava: low-level R to Java interface. R package version 0.8-8 [Cited 1 April 2012.] Available from URL: <http://CRAN.R-project.org/package=rJava>
- VanDerWal J., Shoo L. & Januchowski S. (2010) SDMTTools: Species Distribution Modelling Tools: tools for processing data associated with species distribution modelling exercises. R package version 1.1 [Cited 1 April 2012.] Available from URL: <http://CRAN.R-project.org/package=SDMTTools>
- VanDerWal J., Shoo L. P. & Williams S. E. (2009) New approaches to understanding late quaternary climate fluctuations and refugial dynamics in Australian wet tropical rain forests. *J. Biogeogr.* **36**, 291–301.
- Yates C. J., Elith J., Latimer A. M. *et al.* (2010) Projecting climate change impacts on species distributions in mega-diverse South African Cape and Southwest Australian floristic regions: opportunities and challenges. *Austral Ecol.* **35**, 374–91.
- Yee T. W. & Mitchell N. D. (1991) Generalized additive models in plant ecology. *J. Veg. Sci.* **2**, 587–602.
- Ysebaert T., Meire P., Herman P. M. J. & Verbeek H. (2002) Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. *Mar. Ecol. Prog. Ser.* **225**, 79–95.