

## Research

### Identifying in situ climate refugia for plant species

John B. Baumgartner, Manuel Esperón-Rodríguez and Linda J. Beaumont

*J. B. Baumgartner* (<http://orcid.org/0000-0002-8898-0300>) ([john.baumgartner@mq.edu.au](mailto:john.baumgartner@mq.edu.au)), *M. Esperón-Rodríguez* and *L. J. Beaumont*, Dept of Biological Sciences, Macquarie Univ., NSW, Australia.

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Identification of refugia from climate change is increasingly considered important for biodiversity conservation, but the distribution of putative refugia may vary across alternative climate scenarios, impeding conservation decision-making. Based on 117 plant species representative of ecoregions within south-eastern Australia, we provide a case study identifying in situ refugia across a spectrum of plausible future climates. We define in situ refugia as areas that currently contain populations of the target species, and are projected to remain climatically suitable in the future. Refugia were identified across scenarios describing futures that are, relative to 1990–2009, warmer and wetter, warmer/drier, hotter/wetter, and hotter with little precipitation change. Despite substantial variation in the spatial extent and longevity of climate refugia across species, ecoregions and climate scenarios, clear patterns emerged. By 2070, refugia for species in 1) deserts and xeric shrublands; 2) mediterranean forests, woodlands and shrublands; and 3) temperate and tropical grasslands are likely to be least extensive under a hotter/wetter future. Conversely, wetter conditions may lead to broader refugia for species in temperate forests. We identified areas of congruence where high richness refugia (refugia for  $\geq 50\%$  of representative species) were projected to occur irrespective of the climate scenario. These regions therefore appear robust to uncertainty about climate change, presenting clear targets for conservation attention. Our approach provides valuable information for decision-makers, enabling them to identify and visualise the spatial arrangement of refugia under contrasting scenarios of environmental change. This reveals management options in the context of climate uncertainty and facilitates informed prioritisation of conservation resources.

Keywords: Australia, climate change, conservation, Maxent, NARClIM, species distribution model

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#### Introduction

By the end of the century climate zones will be rearranged. Novel conditions will emerge, with some climate profiles disappearing completely (Williams and Jackson 2007, Beaumont et al. 2011, Radeloff et al. 2015). These changes will undoubtedly have substantial ramifications for biodiversity. Historically, long-term persistence of



populations was favoured by their capacity to adapt to, or migrate away from, harsh conditions (Pearson 2006, Loarie et al. 2009). However, contemporary climate change is occurring at a pace that may exceed the adaptive capacity of many populations and species (Field et al. 2014), and landscape fragmentation may hamper the ability of organisms to track spatial shifts in climate zones (Vos et al. 2008).

During historical periods of climatic instability, the persistence of species unable to keep pace with environmental change was facilitated by the presence of refugia, within which relictual populations survived (Hewitt 1999, Tzedakis et al. 2002, Correa-Metrio et al. 2014, Gavin et al. 2014). Refugia have been defined as regions that maintain favourable conditions absent in the surrounding landscape (Dobrowski et al. 2011, Keppel et al. 2012). They provide protection from regional disturbances and stresses imposed by climate change, and may confer advantages with respect to biotic interactions such as predation, herbivory or competition (Sebens 1982, Brown 2003, Magoulick and Kobza 2003, Beschta 2005). Refugia therefore facilitate the persistence of organisms and other valued resources during extreme climate change (Médail and Diadema 2009, Morelli et al. 2016).

There are two key classes of climate refugia, defined by their spatial relationship with species' known distributions. Ex situ refugia are located in areas that will remain suitable according to scenarios of change, but which are currently uninhabited by the species (Loarie et al. 2008, Ashcroft 2010). In contrast, in situ refugia are regions currently suitable for and inhabited by the species, and are projected to retain suitable conditions while the climate changes (Ashcroft 2010). In situ refugia may arise as a result of range contraction or incomplete range shifts (Gavin et al. 2014). In particular, these refugia may facilitate persistence of existing populations (Lacourse et al. 2003, Loarie et al. 2008, Ashcroft et al. 2009, Patsiou et al. 2014), and may therefore act as reservoirs of biodiversity during eras of climatic instability (Lacourse et al. 2003, Correa-Metrio et al. 2014).

The potential for refugia to mitigate the effects of climate change and safeguard the persistence of biodiversity is an important consideration for climate change adaptation planning (Noss 2001, Taberlet and Cheddadi 2002, Ashcroft 2010, Game et al. 2011, Groves et al. 2012, Keppel et al. 2015, Maher et al. 2017, Mokany et al. 2017). By conserving climate refugia, ecological and evolutionary factors are captured, facilitating population persistence and thereby promoting conservation of biodiversity (Groves et al. 2012). Further, sites that were also refugia during historical climate change are likely to contain endemic and threatened species (Reside et al. 2013, Harrison and Noss 2017), implying some level of irreplaceability and thus further enhancing their conservation value. Where possible, including climate refugia in reserves and connecting them to surrounding habitats is a sensible conservation strategy (Maher et al. 2017, Mokany et al. 2017). Formal decision analysis can be valuable here, allowing land managers to prioritize conservation action (e.g. reserve design) according to the relative benefit of

protecting alternative refugia (V. Graham et al. pers. comm.). However, uncertainty about the complexities of future climate (Fatichi et al. 2016) and the velocity of environmental change (Loarie et al. 2009, Ohlemüller 2011) poses major challenges for conservation practitioners. Therefore, ensuring the persistence of communities and species requires adaptation strategies that are robust to uncertainty about future climate.

Historical refugia can be identified through the use of genetic studies (Hewitt 2000, Maggs et al. 2008, Provan and Bennett 2008), remote sensing (e.g. greenness dynamics; Mackey et al. 2012), and pollen/fossil records (Tzedakis et al. 2002, Correa-Metrio et al. 2014). Other methods define refugia as areas of climatic stability (Sandel et al. 2011, Carroll et al. 2015), or areas with environmental conditions tolerated by the focal species (Loarie et al. 2008, VanDerWal et al. 2009, Reside et al. 2013). Conveniently, these approaches can be applied in the context of environmental dynamics, and so are useful when forecasting the future distribution of refugia under climate change.

Species distribution models (SDMs) are the primary means of estimating species' responses to environmental gradients. These models estimate environmental suitability for species based on the assumption that the environmental tolerances and preferences of species are described by the location of their current populations (Guisan and Thuiller 2005, Elith and Leathwick 2009, Franklin 2010). SDMs can be projected onto past and future climate scenarios to estimate habitat suitability under those conditions. Thus, when spatiotemporal data describing environmental conditions are available for time points of interest, an SDM can be projected to those data to reveal areas with persistent habitat for the modelled species (i.e. refugia) (VanDerWal et al. 2009, Ashcroft 2010, Reside et al. 2013). However, the decision about which climate scenario(s) to use is frequently based on convenience (Evans et al. 2014), and chosen scenarios may not necessarily be derived from climate models that perform well across a region of interest (i.e. can accurately simulate historical conditions). Further, projection onto a single or limited number of climate scenarios may not reflect the range of uncertainty in future conditions that has been captured by a broader set of models. Hence, consideration of a greater number of climate futures may be necessary to capture the range of possible impacts.

To this end, climate uncertainty can be explicitly incorporated into SDM analyses in several ways. Models can be projected onto a broad range of climate scenarios, yielding a set of predictions that better represents the plausible range of impacts. Unfortunately, computational constraints may render this approach infeasible, particularly for studies investigating outcomes for a large number of species. Instead, climate projections from multiple climate models can be summarised into a smaller number of representative scenarios. For example, an assessment of climate refugia for Australian vertebrates summarized the output of 18 climate models by calculating the 10th, 50th, and 90th percentiles of their

projections (Reside et al. 2013). In this case, impacts need only be evaluated for three alternative futures, representing the median and spread of the climate scenarios considered. However, these summaries may reflect conditions that are inconsistent with any particular climate model, or that are highly unlikely to occur (Beaumont et al. 2008).

Instead, the suite of climate scenarios can be simplified to a set that captures a range of relevant, qualitatively contrasting futures. For instance, after assessing the performance of 23 climate models over south-eastern Australia, those climate models with poor skill in simulating historical climate were excluded, and the remaining climate models ranked based on their independence (Evans et al. 2014). This approach enabled identification of a group of models that spanned the broadest range of plausible futures. Rankings were mapped onto a biplot of future climate space framing changes in temperature, from warm to hot (relative to the baseline) and precipitation from decline to increase. A climate model from each of the four quadrants was then identified. These scenarios are now being used for a broad range of impacts assessments (Ofori et al. 2017a, b, V. Graham et al. pers. comm.). Importantly, variation across the resulting modelled impacts clearly captures uncertainty associated with future climate, and enables visualisation of spatial patterns of agreement about, in the case of SDMs, the distribution and suitability of habitat.

In this case study of south-eastern Australia, we demonstrate a novel approach to identifying and prioritising refugia that is readily applied to other taxa and locations. Uncertainty is prevalent in conservation science, and we account for climatic uncertainty by considering contrasting, plausible climate change scenarios that have undergone a rigorous selection process (Evans et al. 2014). Importantly, this approach contextualises climate uncertainty by revealing areas for which predictions of climatic suitability are more or less reliable. We define *in situ* refugia as regions that are currently suitable for and inhabited by representative species (defined below), and that will remain suitable under future climate. Refugia contrast to areas of vulnerability, which are regions that currently harbour populations but are projected to become unsuitable in the future. Specific aims of this study were to identify a) *in situ* climate refugia (hereafter referred to as 'refugia') for representative plant species within each of six ecoregions, with a particular focus on 'high richness refugia' (defined below), and b) areas that may cease to provide suitable conditions for these species ('areas of vulnerability').

## Methods

### Study area

Our study area is the state of New South Wales (NSW) in south-eastern Australia, which spans an area of ~809 450 km<sup>2</sup>. The Great Dividing Range, Australia's most substantial mountain range (500 to 2228 m a.s.l.), runs through the state parallel to the narrow coastal plain. Annual

precipitation varies widely throughout the state. The north-western arid region receives, on average, less than 300 mm of precipitation per year, while the alpine region in the south and the eastern coastal fringe are the wettest areas, with up to ~2350 mm yr<sup>-1</sup>. Mean summer maximum temperatures range from ~15°C in the alpine region to ~35°C in the north-west, while mean winter minimum range from -5°C in the few high altitude areas, to ~7–10°C along the east coast. Frequent frosts and limited snowfall occur in the coldest areas (< [www.bom.gov.au](http://www.bom.gov.au) >).

Within NSW, six broad ecoregions have been defined by the Interim Biogeographic Regionalisation for Australia (IBRA ver. 7; IBRA 2012), derived from ecoregions delineated by Olson et al. (2001), to facilitate conservation planning at large spatial scales. Ecoregions typify different biotas (Dasmann 1973, 1974, Udvardy 1975) and are identified as areas of outstanding biodiversity and representative communities (Noss 1992). Ecoregions reflect the distributions of a broad range of distinct groups of plants and animals since they are based on biogeographical, taxonomic and ecological concepts (Olson and Dinerstein 1998, Olson et al. 2001). The ecoregions present in NSW are: Deserts and Xeric Shrublands (hereafter DXS; ~71 950 km<sup>2</sup>); Mediterranean Forests, Woodlands and Scrub (MFWS; ~79 520 km<sup>2</sup>); Montane Grasslands and Shrublands (MGS; ~5175 km<sup>2</sup>); Temperate Broadleaf and Mixed Forests (TBMF; ~286 175 km<sup>2</sup>); Temperate Grasslands, Savannas and Shrublands (TGSS; ~304 400 km<sup>2</sup>); and Tropical/Subtropical Grasslands, Savannas and Shrublands (TrGSS; ~56 300 km<sup>2</sup>) (Fig. 1).

### Modelling approach

Our aims were to identify a) *in situ* climate refugia (hereafter referred to as 'refugia') for representative plant species (defined below) within each of the six ecoregions, with a particular focus on 'high richness refugia' (HRR; areas where habitat for at least 50% of representative species – defined below – is projected to remain climatically suitable), and b) areas that may cease to provide suitable conditions for these species ('areas of vulnerability'). Each of the above were assessed under four alternative climate futures (described below).

Our approach is summarised as follows. We identified representative plant species within each ecoregion. We obtained spatial data describing climate and soil characteristics for the study area, and used these to fit correlative SDMs. Next, we projected SDMs onto spatial predictor data to estimate current and future habitat for each representative species within each ecoregion. After assessing model accuracy, we created binary maps indicating suitable/unsuitable habitat for each species, masking the spatial extent of suitable habitat to include only those areas in proximity to sites at which occurrences have been recorded (i.e. areas considered 'in situ').

### Target species

We focus on plant species that are broadly representative of the ecoregions. Representative species can play a key role in

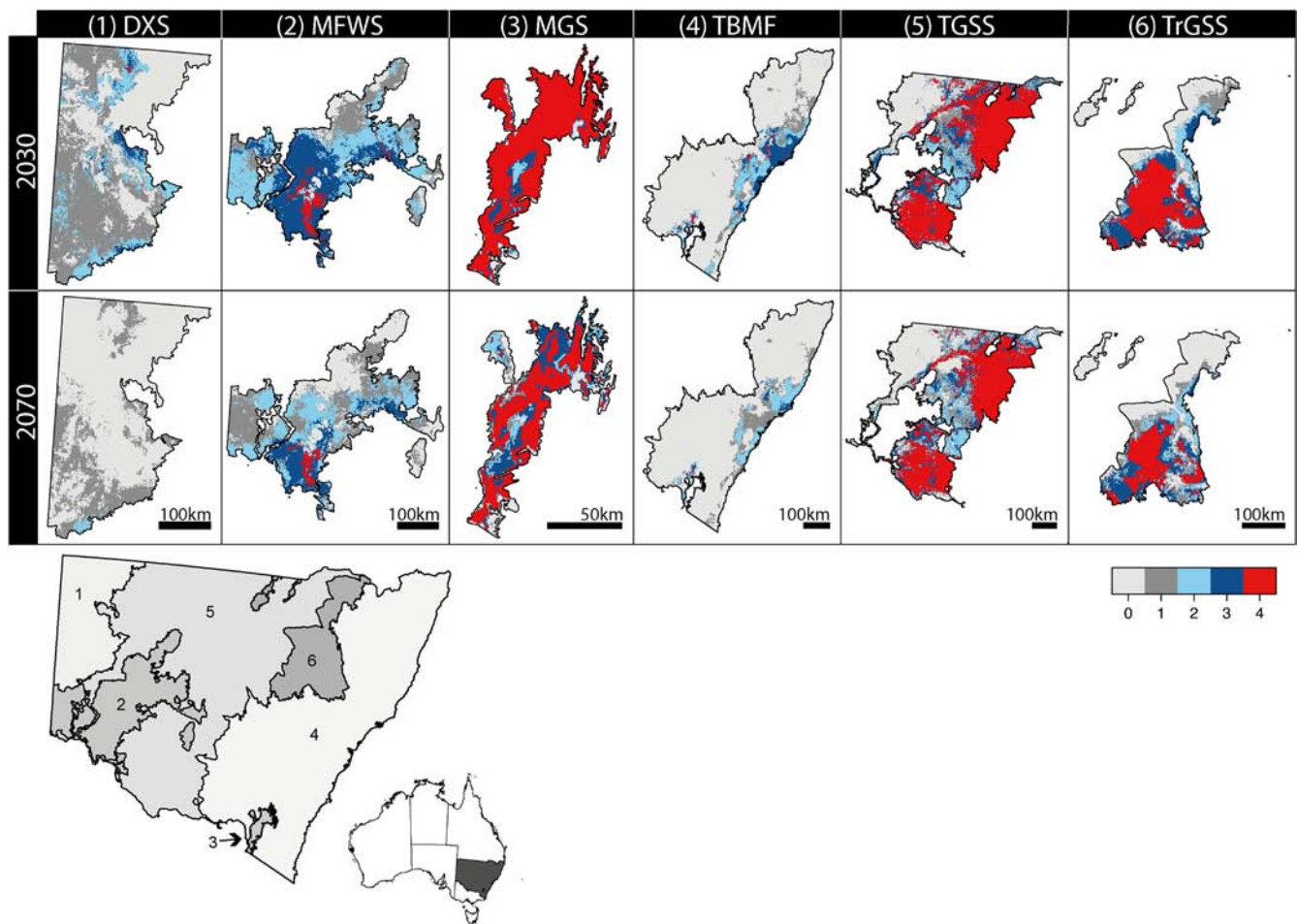


Figure 1. Distribution of in situ refugia across ecoregions in New South Wales. Shown is the extent of agreement across four future climate scenarios about which areas represent high richness in situ climate refugia (HRR), defined as areas that remain suitable for at least 50% of the ecoregion's representative species. Compared to mean annual temperature and annual precipitation for the period 1990–2009, the climate scenarios included are hotter with little precipitation change; hotter and wetter; warmer and drier; and warmer and wetter. The legend indicates the number of future climate scenarios under which a given cell is projected to meet this criterion. DXS = Deserts and Xeric Shrublands; MFWS = Mediterranean Forests, Woodlands and Shrublands; MGS = Montane Grasslands and Shrublands; TBMF = Temperate Broadleaf and Mixed Forests; TGSS = Temperate Grasslands, Savannas and Shrublands; TrGSS = Tropical/Subtropical Grasslands, Savannas and Shrublands.

ecosystems' processes and functioning (Grime 1998). Because these species represent a larger group of species and associated habitats within landscapes across a given region, focussing on them can simplify conservation decision-making (Caro and O'Doherty 1999, USFWS 2012). An important assumption around the use of representative species is that conservation actions targeting them will also cater to other species within the communities they represent (Lambeck 1997, Noon et al. 2009, USFWS 2012). We point out, however, that a variety of approaches can be undertaken for selecting species for which to identify refugia, and that the most appropriate method may vary depending upon the goals of the particular study.

We used occurrence records from the NSW Office of Environment and Heritage Wildlife Atlas (OEH Atlas) to identify the 30 most commonly recorded native plant species for each of the six ecoregions. This led to 154 unique

species (some species were among the most common in more than one ecoregion). We filtered this list to retain only those species noted as representative (characteristic, abundant, or otherwise prominent) of floristic communities across the state (Keith 2004). The final list totalled 117 species (Supplementary material Appendix 1 Table A1), with 24 species in DXS, 27 species in MFWS, 11 species in MGS, 23 species in TBMF, 28 species in TGSS, and 28 species in TrGSS.

For each of the 117 representative plant species, OEH Atlas occurrence records were supplemented by records obtained from the Australia's Virtual Herbarium (AVH) hub of the Atlas of Living Australia (ALA, < www.ala.org.au >), a database comprising records arising from incidental observations and planned surveys. We used occurrence data from species' entire Australian ranges, rather than restricting our analysis to the subset of records from NSW. This approach



captures each species' entire realised niche within Australia. We cleaned occurrence data before use, removing records that met any of the following criteria: recorded prior to 1950; not georeferenced; coordinate uncertainty greater than 1000 m; invalid coordinate reference system; noted by ALA as a spatial/environmental outlier or duplicate record; having invalid scientific name; or being cultivated. The AVH data were limited to records with associated voucher specimens, for which taxonomic identity is more certain. Finally, records for each species were overlaid on a  $1 \times 1$  km raster grid (see Climate data) and reduced to a single point per species per cell. This resulted in between 37 and 8543 records per species (mean  $\pm$  SD =  $2350.6 \pm 2044.2$ ; DXS =  $1133.9 \pm 1224.9$ ; MFWS =  $1378.2 \pm 1133.1$ ; MGS =  $476.7 \pm 461.1$ ; TBMF =  $4779.7 \pm 1881.8$ ; TGSS =  $2422.6 \pm 1544.1$ ; TrGSS =  $3960.9 \pm 1871.9$ ).

### Climate data

We used current and future climate data generated by the NSW and ACT Regional Climate Modelling (NARCLiM) project (Evans et al. 2014). The standard set of 19 bioclimatic variables (BIOCLIM; Busby 1991) was obtained at 0.01 degree ( $\sim 1$  km) resolution (Hutchinson and Xu 2014) for baseline climate (1990–2009), near-future (2020–2039) and distant future (2060–2079). We considered the three periods to be representative of the long-term average climate around their midpoints: 2000, 2030, and 2070. These data were derived from NARCLiM climate surfaces projected by four CMIP3 (Meehl et al. 2007) Global Climate Models (GCMs; specified below), each of which was dynamically downscaled to 0.1 degree resolution using three configurations of the Weather and Research Forecasting (WRF ver. 3; Skamarock et al. 2008) Regional Climate Model (RCM). The GCMs assumed the SRES A2 emissions scenario (Nakicenovic et al. 2000), which roughly follows the trajectories of the newer RCP8.5 scenario in terms of projected radiative forcing and global mean annual temperature (i.e. high emissions; IPCC 2013).

The projections of the resulting 12 models (i.e. four GCMs, each downscaled using three RCMs) encompass a range of equally plausible climate futures for south-eastern Australia (Evans and Ji 2012). Broadly, relative to baseline (1990–2009) mean annual temperature and annual precipitation, MIROC3.2(medres) projects a future that is warmer and wetter, particularly in the north-east of the state, although alpine regions are projected to become drier. CCCMA CGCM3.1(T47) projects a future hotter than MIROC3.2(medres), and one that is also wetter across most of the state. CSIRO-Mk3.0 projects a future warmer than the baseline period, and is generally the driest of the four models. ECHAM5/MPI-OM projects the greatest increase in temperature, with changes in precipitation varying across the state (slightly wetter in the north-west and coastal regions and slightly drier elsewhere) (Supplementary material Appendix 1 Fig. A1–A4). Hereafter we refer to the scenarios as warmer/wetter (MIROC3.2(medres)), hotter/wetter (CCCMA

CGCM3.1(T47)), warmer/drier (CSIRO-Mk3.0), and hotter/little change (ECHAM5/MPI-OM).

Finally, climate data were transformed to the Australian Albers Equal-Area Conic projection (EPSG:3577) at 1 km resolution using bilinear interpolation.

### Static environmental data

To supplement climate predictors, we used data describing soil attributes derived from measurements of the spectra of surficial (0–20 cm depth) topsoils (Viscarra Rossel and Chen 2011). These continuous data represent the first three principal components from a principal components analysis performed on spectral characteristics of soil samples from across Australia. They therefore contain information about fundamental soil characteristics, including colour, particle size, and amount of clay, iron oxide, organic matter, and water, which are likely to influence plant species' distributions (Viscarra Rossel and Chen 2011). In particular, the first principal component describes the distribution of highly weathered soils, the second describes the distribution of soils with large amounts of organic matter, and the third reflects the distribution of low relief landscapes with soils containing abundant smectite (clay) minerals (Viscarra Rossel and Chen 2011). These gridded data were obtained from the Soil and Landscape Grid of Australia ([www.clw.csiro.au/aclep/soilandlandscapegrid](http://www.clw.csiro.au/aclep/soilandlandscapegrid)). Initially provided at 3 arc-second ( $\sim 90$  m) resolution, we projected these grids to the Australian Albers Equal-area Conic projection and aggregated them to  $1 \times 1$  km by calculating the average of contributing cells. When generating projections of future habitat suitability (section Current and future habitat suitability), soil predictors were assumed to remain static. While we recognise that some soil attributes will change over relatively short time spans, data describing future states were unavailable, and several studies have demonstrated that including edaphic variables can enhance SDMs' predictive capacity (Austin and Van Niel 2011, Bertrand et al. 2012, Stanton et al. 2012, Dubuis et al. 2013, Hageer et al. 2017).

### Species distribution models

We selected a subset of the BIOCLIM predictors to be used for all plant models. This set included: 1) mean diurnal temperature range; 2) temperature seasonality (the coefficient of variation of weekly mean temperature); 3) maximum temperature of the warmest week; 4) minimum temperature of the coldest week; 5) precipitation of the wettest week; 6) precipitation of the driest week; and 7) precipitation seasonality (the coefficient of variation of weekly total precipitation). These represent a common set of climatic variables that influence ecophysiological functions, and thus species' distributions.

We modelled habitat suitability with Maxent 3.3.3k (Phillips et al. 2006, Elith et al. 2011), a machine learning approach to species distribution modelling known for its superior performance (Elith et al. 2006). A fitted Maxent

model can be projected to spatial environmental data, producing continuous scores indicating the relative environmental suitability with respect to the included predictors. Locations with higher values are deemed to have greater suitability for the modelled species (Phillips et al. 2006, Phillips and Dudik 2008). Detailed descriptions of Maxent are given elsewhere (Elith et al. 2011, Merow et al. 2013).

Models were fit using default settings, besides disabling hinge and threshold features to avoid locally-overfit response curves. Absence data were unavailable for this study, and it is highly likely that occurrence records sourced from natural history collections represent spatially- or environmentally-biased samples. To handle this bias, we used a buffered target-group background (Elith and Leathwick 2007, Phillips and Dudik 2008). That is, our background samples comprised random subsets of up to 100 000 cells from the pool of cells that contained native plant occurrence records (of any native Australian plant species) and fell within 200 km of records for the target species.

Performance was estimated for each model by calculating the average test AUC (the area under the receiver operating characteristic curve; Swets 1988) through five-fold cross-validation. This involved splitting occurrence data into five subsets (i.e. folds) of roughly equal size, fitting the model to four of the five folds and predicting to the fifth. This process was repeated until each fold was used four times for model fitting and once for model evaluation (Stone 1974). Following this, models for each species were fit a final time using the complete set of occurrence data, and these final models were used for subsequent analyses.

### Current and future habitat suitability

Habitat suitability for each species was estimated for 2000, as well as for the 12 alternative future climates for both 2030 and 2070, by projecting final fitted models onto spatial data representing the corresponding states of climate and soil predictors. Continuous suitability predictions were then converted to binary layers indicating suitable/unsuitable habitat, with thresholds chosen to maximise the sum of sensitivity and specificity, a frequently recommended approach that tends to reflect the prevalence of the modelled species well (Jiménez-Valverde and Lobo 2007, Liu et al. 2013, 2016). The three RCMs belonging to each GCM were aggregated by consensus, considering a cell to be suitable only if it was suitable under all three RCMs. We recognise that this represents a cautious approach to identification of suitable habitat, as is appropriate when identifying the sites most likely to serve as refugia. This approach led to four alternative projections of suitability (one per GCM) for each time period.

For each map of suitable habitat for a given species, we restricted our analysis to the ecoregions for which that species was amongst the most prevalent (i.e. the species was representative of those ecoregions). To determine whether suitable cells formed in situ refugia within these ecoregions, we excluded areas that were evidently unpopulated (and hence ex situ). To achieve this, we considered IBRA subregions,

smaller spatial units contained within ecoregions, defined by common climate, geology, landform, and vegetation (IBRA 2012). These subregions delineate appropriate areas for assessing and planning for the protection of biological diversity and land conservation (Thackway and Cresswell 1995, Cummings 2000). We considered any IBRA subregion as being within the modelled species' range if it contained occurrence points for the species. Conversely, we excluded subregions that were classified as suitable but for which no occurrence records existed. In doing so we make the assumption that these areas, although deemed suitable, are not known to contain extant populations of the target species and therefore fall outside our definition of in situ refugia and areas of vulnerability. This approach to defining in situ habitat was preferable to a grid-cell based approach, as the latter would severely underestimate the distribution of refugia, restricting them to individual cells that contained persisting suitable habitat for at least 50% of representative species.

Finally, for each ecoregion we calculated the number of representative species currently in each IBRA subregion and the proportion of these for which suitable climate remains under each of the four climate futures. We then identified subregions projected to a) retain  $\geq 50\%$  of their representative species (HRR), and b) lose  $\geq 50\%$  of their representative species (areas of vulnerability) under individual climate futures and across all four.

All modelling and calculation of statistics was performed in R ver. 3.1.2 (R Development Core Team). We used the ALA4R package (Raymond et al. 2015) to obtain species occurrence records from ALA, the gdalUtils (Greenberg and Mattiuzzi 2015), rgeos (Bivand and Rundel 2016), sp (Pebesma and Bivand 2005), and raster (Hijmans 2015) packages for representation, comparison, and manipulation of spatial data, the dismo package (Hijmans et al. 2016) to fit Maxent models, and custom R code for rapid projection of fitted models.

## Results

Across the 117 species, average cross-validated test AUC ranged from 0.77 ( $\pm 0.004$ ) (*Pomax umbellata*) to 0.99 ( $\pm 0.006$ ) (*Chionochoa frigida*), indicating high classifier performance (Supplementary material Appendix 1 Table A1) (Swets 1988). Contributions of variables to the model (permutation importance, reported by Maxent) are shown for each species in Supplementary material Appendix 1 Fig. A17.

### Projected changes in suitable habitat for representative species

Our goal was to identify putative in situ refugia. By definition, the geographic extent of these areas, relative to the baseline period, can remain stable or decline. Expansion cannot occur. That is, sites classified as refugia in 2030 must be occupied in 2000, and suitable in both periods. To remain refugia in 2070, sites must be occupied in 2000 and suitable in 2030 and 2070.

Averaged across all 117 species, refugia in the near (2030) and distant (2070) future were projected to be most extensive under the warmer/wetter scenario (encompassing on average  $70.2 \pm 20.5\%$  [SD] of current habitat by 2030, and  $55.9 \pm 26.3\%$  by 2070) (Fig. 2 and 3). In contrast, the combined extent of refugia was smallest under the hotter/wetter scenario (2030:  $52.4 \pm 30.9\%$ ; 2070:  $43.9 \pm 32.1\%$ ). By 2070, between eight (warmer/wetter) and 23 (hotter/wetter) species were projected to have in situ refugia that span  $<10\%$  of current habitat. In contrast, for 11–14 species,  $>90\%$  of current habitat was projected to be refugial.

Across the 24 species representative of DXS, the median proportion of current habitat projected to offer refugia in 2030 ranged from 66.5% (hotter/wetter) to 78.9% (warmer/wetter) (Fig. 2, Supplementary material Appendix 1 Fig. A5 and A11). Current habitat will likely remain very stable for several species:  $>95\%$  of current habitat was projected to be retained until at least 2070 for *Senna artemisioides*, *Sclerolaena lanicuspis*, and *Acacia victoriae*, regardless of climate scenario. Conversely, *A. ligulata*, *A. loderi*, and *Maireana sedifolia* were projected to have limited, if any, refugia in the majority of climate scenarios.

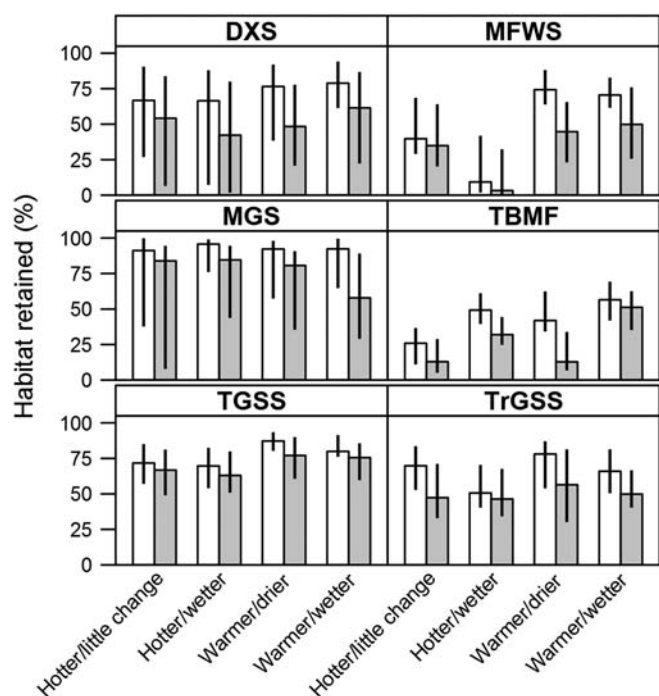


Figure 2. The proportion of currently suitable in situ habitat that remains suitable at 2030 (white bars) and at 2070 (grey bars). Results are presented for each ecoregion, and for each of four global climate models (hotter, with little precipitation change; hotter/wetter; warmer/drier; warmer/wetter, compared to mean annual temperature and annual precipitation for the period 1990–2009). Note that this is equivalent to the proportion of habitat that is considered to be in situ refugia. Bar height indicates the median across species representative of the ecoregion, and error bars show the 25th and 75th percentiles. Ecoregion abbreviations are as in Fig. 1.

The size of projected refugia in MFWS for the 27 representative species varies greatly across climate scenarios, spanning a median of 9.3% under the hotter/wetter scenario, to 74.3% under the warmer/drier scenario (Fig. 2, Supplementary material Appendix 1 Fig. A6 and A12). Only one species, the shrub *S. artemisioides*, is projected to retain all current habitat by 2070, regardless of climate scenario; whereas refugia are projected to span  $<10\%$  of current habitat for 15 species under the hotter/wetter scenario.

MGS is the smallest ecoregion within NSW. While we refer to climate scenarios by the titles stated in Methods (e.g. warmer/wetter; warmer/drier, etc.), most scenarios project drying across MGS (Supplementary material Appendix 1 Fig. A1 and A2). Substantial refugia were predicted for all 11 species representative of MGS, with  $>90\%$  of current habitat remaining suitable by 2030 for five species under all climate scenarios (Fig. 1, 3, Supplementary material Appendix 1 Fig. A7 and A13). Generally, little habitat loss was projected for the representative *Eucalyptus* species, but refugia are less extensive for ground cover species.

TBMF is vast, spanning the latitudinal extent of the state and including the entirety of the heavily urbanised eastern seaboard. For the 23 representative species, refugia by 2030 are projected to occupy between 25.9% (median for hotter/little change scenario) to 56.5% (warmer/wetter scenario) of current habitat (Fig. 2, Supplementary material Appendix 1 Fig. A8 and A14). While there is substantial variation in projections for individual species, there are no species that either retain, or lose, most of their current habitat across all four scenarios.

Within the TGSS, four species (*Acacia stenophylla*, *Eucalyptus coolabah*, *E. camaldulensis*, and *Eremophila mitchellii*) were projected to retain at least 95% of current habitat by 2030, regardless of scenario. Few species were projected to lose  $>50\%$  of their habitat in the same time frame. Refugia at 2030 were projected to span 67.5% (median under hotter/wetter) to 87.3% (warmer/drier) of current habitat (Fig. 2, Supplementary material Appendix 1 Fig. A9 and A15).

By 2030, refugia in TrGSS were projected to range from 50.6% (median under hotter/wetter) to 78.1% (warmer/drier) of current habitat (Fig. 2, Supplementary material Appendix 1 Fig. A10 and A16). All representative species were projected to retain refugia across all scenarios, although for some species substantial variation was evident. For example, 2030 refugia for the spear-grass *Austrostipa verticillata* is restricted to  $<25\%$  of its current distribution under the hotter/wetter scenario, but  $>85\%$  under the warmer/drier scenario.

We identified ‘high richness refugia’ (HRR) – areas projected to retain refugia for at least 50% of their representative species. There was little overlap across the four scenarios in the location of HRR in DXS. Although HRR are projected across the southern region of DXS under the warmer/wetter scenario for 2030, these areas fragmented substantially by 2070 (Fig. 1 and 3). A key area of vulnerability lies in the south-east of this ecoregion, i.e. this area currently supports



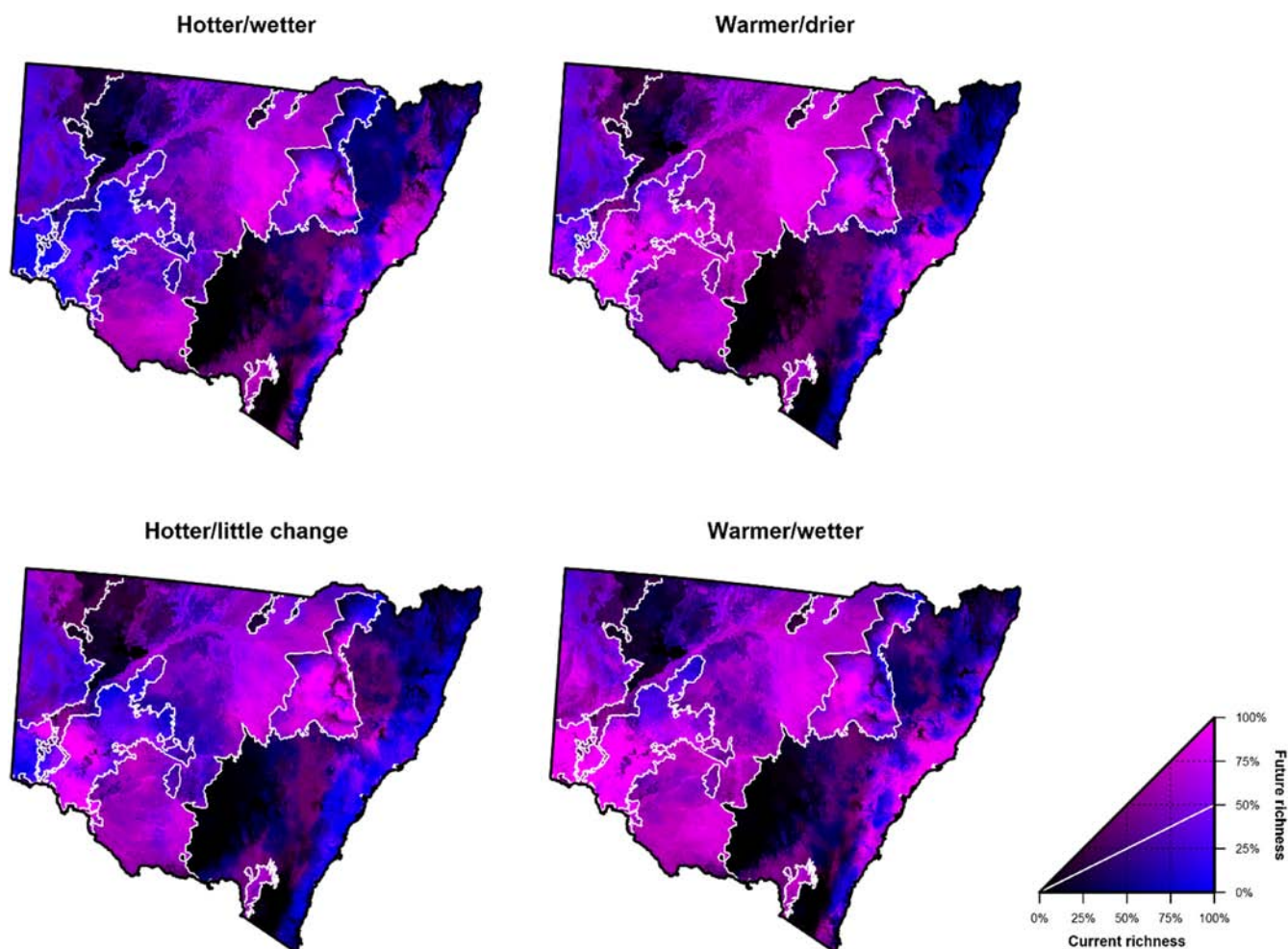


Figure 3. Climate refugia and areas of vulnerability across New South Wales under four future climate scenarios for 2030 (hotter, with little precipitation change; hotter/wetter; warmer/drier; warmer/wetter, compared to mean annual temperature and annual precipitation for the period 1990–2009). Colours are interpreted as in the triangular legend at right, which shows current and future richness as a proportion of the number of representative species for each of the six ecoregions (which ranges from 11–27). Purple colours (above the white line in the legend) indicate that habitat is retained for more than 50% of initially occurring, representative species, while blue colours (below the white line) indicate that habitat is lost for more than 50% of initially occurring, representative species. Darker colours indicate that initial richness was low relative to the pool of representative species. Bright blue indicates vulnerable high-richness areas (i.e. where current richness is high, but future richness is low); dark blue indicates vulnerable low-richness areas (current richness is low, future richness is lower); bright purple areas indicate high richness refugia (HRR; both current and future richness are high); and dark purple indicates low richness refugia (current richness is low but maintained into the future). Supplementary material Appendix 1 Fig. A11–A16 show enlarged maps for each ecoregion, for both 2030 and 2070.

a high proportion of representative species but is projected to be unsuitable for most by 2070.

For MFWS, HRR are projected to be extensive under the two warmer scenarios, spanning most of the ecoregion by 2030, and including numerous protected areas. By 2070, contraction of HRR is projected in the north under the warmer/wetter scenario, and in central and western regions under the warmer/drier scenario (Fig. 1 and 3). However, a large, contiguous area of HRR was predicted in the south under all four scenarios.

HRR were also projected throughout much of the MGS in 2030, under both wetter scenarios. By 2070, however, lower altitude margins are no longer projected to be HRR,

and less agreement occurs among scenarios (Fig. 1 and 3). Conversely, HRR in the TBMF are mostly limited to small areas in the central coastal zone, although these regions are more extensive and persistent under the wetter scenarios. There is generally little overlap in the placement of HRR across scenarios (Fig. 1), and key areas of vulnerability in the north and south of this ecoregion (Fig. 3) include numerous large, well-connected protected areas.

In TGSS, HRR were projected to remain extensive by 2070, particularly under the warmer scenarios (Fig. 1 and 3). Considerable overlap in HRR was evident across the four scenarios, with large contiguous refugia projected in the northeast and south. In contrast, the central region of this



ecoregion (Cobar Penneplains) is likely to be vulnerable, particularly under the hotter scenarios.

In the northern part of the TrGSS, HRR projected under the warmer/drier scenario for 2030 will likely be lost by 2070 (Fig. 1 and 3), making this a key area of vulnerability. In contrast, all scenarios projected HRR in the south, extending across the Pilliga region, although these contract and fragment by 2070.

## Discussion

For climate change impacts assessments to support conservation management and decision-making, potential impacts need to be forecast, summarised and visualised across a range of plausible futures. Here, we demonstrate an ensemble approach to identifying in situ climate refugia for key plant species representative of major ecoregions. We accomplished this by using a set of rigorously-selected scenarios spanning distinct combinations of temperature increase and precipitation change. For our case study system, we found that the hotter/wetter scenario corresponded to the smallest refugial area, while refugia were generally largest under the warmer/wetter scenario. The most vulnerable ecoregions in NSW are MFWS and TBMF, while the species most threatened by loss of suitable habitat under different scenarios are: *Acacia ligulata*, *A. loderi*, and *Maireana sedifolia* (DXS); *Casuarina pauper* and *Sclerolaena obliquicuspis* (MFWS); *Ranunculus anemoneus* and *Chionochloa frigida* (MGS); and *Eustrephus latifolius* and *Oplismenus hirtellus* (TBMF). While our case study focussed on native flora of south-eastern Australia, the approach can be readily extended to other taxa and locations.

### Where are climate refugia in NSW likely to be located?

The location of climate refugia is context-dependent. Although we have focused on representative species, equally valid approaches have identified refugia that cater to endemic or threatened species (Chitale et al. 2014, Meng et al. 2016, Stratmann et al. 2016), capture a set of critical landscape characteristics (Molina-Venegas et al. 2016, Sandberg et al. 2016), or aim to protect genetic diversity (Havrdová et al. 2015, Souto et al. 2015, Lourenço et al. 2016).

Our results indicate that for most of the 117 species included in this study, in situ refugia of varying sizes will exist until at least 2070. In general, however, refugia for individual species in the arid (DXS), mediterranean (MFWS), and grassland (TGSS, TrGSS) ecoregions are likely to be less extensive if a hotter/wetter future prevails. In contrast, refugia for species in the montane (MGS) and temperate broadleaf (TBMF) ecoregions are likely to be more extensive if conditions are generally wetter than present.

Regardless of the location of study, from land management and conservation perspectives, areas where refugia are projected under all four climate scenarios are sensible conservation targets. These areas are robust to future variation in regional climate, leading to high stability in habitat

suitability for the existing species pool. We projected that for some ecoregions, large tracts of high richness refugia (HRR) will persist until at least 2070, irrespective of the climate scenario.

Of particular concern are those ecoregions with limited HRR or with little congruence across climate scenarios. For example, TBMF spans eastern NSW and includes the most heavily urbanised region in Australia. Under most climate scenarios, species representative of this ecoregion are projected to lose a greater proportion of their current habitat than species elsewhere. Another example is the refugia, or lack thereof, along the Great Eastern Ranges (GER). It has been suggested that the GER may play an important role in providing refugia or corridors to aid species migration in response to climate change (DSEWPaC 2012). However, there was a distinct lack of congruence across the four scenarios with respect to the location of HRR along the GER. This does not preclude the value of investing in connectivity corridors across the GER – rather, it highlights the potentially dynamic nature of its ecosystems.

### What are the strengths and limitations of this study?

Our results extend previous studies that have used different approaches to identify climate change refugia for biodiversity across Australia (Reside et al. 2013, Williams et al. 2014). However, in contrast to those studies, our approach identifies areas most likely to serve as climate refugia under a range of qualitatively distinct, but plausible climate futures, for species representative of their respective communities and ecoregions. In doing so, we assume that representative species may be surrogates for dominant (Grime 1998, Loreau et al. 2001) and umbrella (Caro and O’Doherty 1999) species. We hypothesise that retention of suitable habitat currently occupied by representative species will facilitate survival of their populations, and likely cause less disruption to ecosystem function than if conditions were to exceed these species’ tolerances. We also assume that refugia catering for representative species will support a general suite of species native to the area (Cruse et al. 2015), and that their loss may impact ecosystem processes by altering species composition (Brown et al. 2001, Loreau et al. 2001), and may lead to ecosystem instability (Sasaki and Lauenroth 2011). Our results suggested that for some regions, a larger suite of species might be required to adequately represent the enclosed communities. For example, the TBMF region spans a range of distinct community types, and coastal sampling bias may have resulted in an overemphasis on species indicative of coastal communities.

However, this approach also relies on the assumption that biotic interactions involving representative species will be maintained in the future (Ashcroft 2010). Even if this is the case, retention of suitable habitat for representative species does not preclude changes to community composition, since species will respond idiosyncratically to climate change (Pucko et al. 2011, Maharaj and New 2013, Esperón-Rodríguez and Barradas 2015, García-Robledo et al. 2016,

Malyshev et al. 2016). It is also assumed that occurrence records used to identify refugia represent viable populations, and that the minimum viable population size will be accommodated by individual refugia.

Our approach enables identification of areas likely to serve as in situ refugia that are robust to uncertainty about the nature of climate change. However, outside of these in situ refugia, community persistence during climate change may yet be facilitated by micro-refugia too small to be detected at the scale of the environmental data used for model fitting. Further, while our focus on in situ refugia reflects their importance for communities' continued persistence, habitat adjacent to species' current ranges is likely to become suitable through time. Identifying these ex situ (Ashcroft 2010) or 'stepping-stone' (Hannah et al. 2014) refugia may also be essential for achieving conservation goals. While beyond the scope of this study, a focus on such ex situ refugial areas would be a valuable extension of the present work.

Our results may also be sensitive to our methodological decisions. Regions that were predicted to maintain suitable conditions through time, but which lacked occurrence records, were assumed to be ex situ refugia. However, a lack of occurrence records need not imply that a species is absent, particularly for under sampled regions. It is common for the density of occurrence records to decline with distance from coastal urban centres, largely reflecting spatial variation in sampling effort (Haque et al. 2017). This may partly explain the paucity of HRR in the western regions of TBMF that are distant from Sydney.

### **What are the management implications of this study?**

Climate refugia play a critical role in conserving biodiversity by providing relative stability during times of environmental change. Given the importance of climate refugia in ensuring species' persistence through harsh conditions, identifying these areas will support management aimed at climate change adaptation. Our study revealed areas likely to serve as climate refugia for plant communities across varying ecoregions, and indicated whether these refugia were robust to uncertainty about climate change. Our approach highlighted regions where current communities are vulnerable to changing conditions and may undergo change in composition.

The in situ refugia we identified present clear opportunities for management aimed at maintaining ecosystem function under climate change (Loreau et al. 2001). This is particularly true where their value as refugia is evident across multiple climate scenarios. By explicitly considering and conveying the implications of climate uncertainty, outputs such as these can inform strategic management based on formal decision theory (Resnik 1987, Jeffrey 1990, V. Graham et al. pers. comm.). We suggest that while additional (ex situ or stepping stone) refugia may exist beyond species' known distributions, the accessibility of in situ refugia likely renders them more valuable since these areas might be vital for species with poor dispersal capabilities, or whose dispersal is obstructed,

for example by anthropogenic barriers, preventing them from tracking shifting habitat (Ashcroft 2010, Reside et al. 2014). The consideration of ex situ refugia in management plans requires additional assumptions about dispersal and colonisation capacities, and the effectiveness of habitat corridors (Ashcroft 2010), which may be poorly understood for many species.

Temporally-persistent climate refugia accommodating the majority of local representative flora (our HRR) are likely to play a critical role in the long-term endurance of plant communities in the face of climate change. Targeting conservation at regions of higher richness should foster the retention of a diversity of ecosystem services (Chan et al. 2006, Egoh et al. 2009) and resilience to climate change (Oliver et al. 2015). However, when allocating conservation resources to managing such refugia, their suitability with respect to key non-climatic factors should also be considered. We found that climatically-suitable HRR sometimes occurred in landscapes with poor habitat condition (e.g. cleared or degraded areas, or near urban centres). This challenge to prioritisation can be minimised by comparing the spatial arrangement of HRR to spatial data describing general landscape hospitability (e.g. vegetation condition; Drielsma et al. 2015), or by using such data as predictors in habitat suitability models. Habitat quality is thought to relate to resilience to the stress of climate change (Zomer et al. 2008, Field et al. 2014), thus management of HRR in areas of good condition is likely to yield favourable outcomes.

### **Conclusion**

Rapid climate change is one of the greatest threats to ecosystems, particularly when organisms are unable to keep pace via migration or adaptation (Loarie et al. 2009). For some species, in situ climate refugia will present the most viable option for their survival, underscoring the critical importance of identifying, restoring and protecting these areas. Here, we have demonstrated a straightforward and generally-applicable approach to characterising climate refugia, as well as areas vulnerable to community disruption, based on representative species. However, key uncertainties remain. First, without concerted efforts to mitigate climate change, the efficacy of the refugial areas identified in this project will likely decline beyond 2070. Second, to be effective, refugia must afford protection from not just climate-change related stressors, but also non-climatic threatening processes (Reside et al. 2014). Finally, suitable long-term average climate does not preclude unfavourable extreme weather events (Butt et al. 2016). Extensions to the present study would benefit from additionally considering the impact of such extreme events.

Our approach provides valuable information for decision-makers, enabling them to visualise the spatial arrangement of refugia and areas of vulnerability. This approach reveals conservation options in the context of climate uncertainty, and facilitates their prioritisation. Additionally, our methodology identifies areas likely to support community persistence

across the spectrum of plausible climate futures. Our consideration of a range of contrasting climate scenarios provides an explicit approach to contextualising climate uncertainty, thereby facilitating transparent, effective management of biodiversity.

## Abbreviations

DXS – Deserts and Xeric Shrublands; HRR – High Richness Refugia; MFWS – Mediterranean Forests, Woodlands and Scrub; MGS – Montane Grasslands and Shrublands; NSW – New South Wales; RCM – Regional Climate Model; SDM – Species Distribution Model; TBMF – Temperate Broadleaf and Mixed Forests; TGSS – Temperate Grasslands, Savannas and Shrublands; TrGSS – Tropical/Subtropical Grasslands, Savannas and Shrublands.

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Supplementary material (Appendix ECOG-03431 at < [www.ecography.org/appendix/ecog-03431](http://www.ecography.org/appendix/ecog-03431) >). Appendix 1.