Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global warming?

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Abstract

Models that couple habitat suitability with demographic processes offer a potentially improved approach for estimating spatial distributional shifts and extinction risk under climate change. Applying such an approach to five species of Australian plants with contrasting demographic traits, we show that: (i) predicted climate-driven changes in range area are sensitive to the underlying habitat model, regardless of whether demographic traits and their interaction with habitat patch configuration are modeled explicitly; and (ii) caution should be exercised when using predicted changes in total habitat suitability or geographic extent to infer extinction risk, because the relationship between these metrics is often weak. Measures of extinction risk, which quantify threats to population persistence, are particularly sensitive to life-history traits, such as recruitment response to fire, which explained approximately 60% of the deviance in expected minimum abundance. Dispersal dynamics and habitat patch structure have the strongest influence on the amount of movement of the trailing and leading edge of the range margin, explaining roughly 40% of modeled structural deviance. These results underscore the need to consider direct measures of extinction risk (population declines and other measures of stochastic viability), as well as measures of change in habitat area, when assessing climate change impacts on biodiversity. Furthermore, direct estimation of extinction risk incorporates important demographic and ecosystem processes, which potentially influence species' vulnerability to extinction due to climate change.

Keywords: abundance, bioclimate envelope, connectivity, coupled niche-population model, dispersal, habitat suitability, mechanistic model, metapopulation, population viability analysis, species distribution model

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Introduction

The influence of climate change on species' ranges, phenology and physiology has already been widely documented (Parmesan, 2006; Rosenzweig et al., 2008). However, predictions of future extinction risk based on observed effects of climate change at the species level have proven more difficult (Akçakaya et al., 2006; Pereira et al., 2010). This is partly because most current methods for evaluating the effects of climate change on biodiversity, such as correlative species distribution models (SDM), only consider climate-driven changes in geographical range area or the quality and quantity of suitable habitat (Thomas et al., 2004; Araujo et al., 2006). Recent research has attempted to incorporate the mechanisms and interactions that

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drive species distributions and abundance more explicitly (Keith *et al.*, 2008; Anderson *et al.*, 2009; Buckley, 2010; Kearney *et al.*, 2010; Lawson *et al.*, 2010; Fordham *et al.*, 2012). However, it is not known how sensitive measures of change in range area and population abundance are to these modeling details, or how well these proxy risk metrics are correlated with more direct estimates of extinction probability (i.e., assessments of the likelihood of population decline).

Species' ranges are commonly modeled using statistical associations that link species' occupancy or abundance records to spatial environmental variables, implicitly capturing processes that limit the distribution of the species (Elith & Leathwick, 2009). The resulting correlative SDMs (also termed bioclimatic envelope, habitat or ecological niche models) can then be projected onto landscapes to identify geographic regions with potentially suitable environmental conditions. Correlative SDMs are commonly used to draw inferences about future extinction risk of species and suitability of their habitats because they allow exploration of potential future changes in geographic range areas and habitat quality in response to human related disturbances, such as climate change. However, the use of correlative SDMs to predict responses to climate change operates under the assumptions that: (i) observed species distributions are in equilibrium with the climate and habitat factors constraining those distributions; (ii) current climatic and geographic constraints that define a species distribution reflect its biophysical limits; and (iii) a model fitted to current data will project sensibly to new environmental conditions (Franklin, 2010; Peterson *et al.*, 2011).

Whilst correlative SDMs reflect outcomes of ecological processes that affect species, they can only do so implicitly through the spatial patterning of species records. In some instances, species demographic traits may account for a high level of variability in model performance. For example, Dobrowski *et al.* (2011) found that SDMs of plant species with greater dispersal capacities, intermediate levels of prevalence and a weak reproductive response to fire had better future and historical predictive ability than models of plants with limited dispersal capacity that rely on fire for reproduction. Other lines of evidence, based on more mechanistic approaches, also suggest that species traits are important for understanding the dynamics of species ranges in changing environments (Best *et al.*, 2007; Buckley, 2010). Mechanistic approaches that account for demographic processes that drive species' distribution and abundance better approximate observed spatial patterns of abundance and geographic range size (Cabral & Schurr, 2010).

Efforts to adopt more process-based approaches have led to some apparently paradoxical (but important) outcomes that were not detected by correlative approaches alone. For example, spatially structured metapopulation models of South African fynbos plants forecast rapid declines and range contractions in some currently widespread species under future climate change, while other species that are currently restricted were predicted to stay relatively stable, or even expand their distributions (Keith *et al.*, 2008). Although mechanistic techniques, such as linking correlative SDM forecasts to structured spatial population models, may be more realistic on *a priori* grounds (Brook *et al.*, 2009), whether predictive accuracy is actually enhanced will depend on how well the demographic (or physiological) component of the model captures the ecology of the species. Thus, correlative SDMs, which are much simpler to parameterize and computationally less intensive than coupled approaches, might be better suited to some circumstances. Model evaluations using well-studied organisms are therefore required to test the predictive ability of correlative SDM-only approaches, and compare model performance with coupled SDM-population models (*coupled niche-population models*).

The IUCN Red List (IUCN, 2010b) is the most widely used global threatened species list, using quantitative criteria based on estimates of habitat change, as well as more direct measures of extinction risk (Rodrigues *et al.*, 2006). Difficulties in applying the criteria to species affected by global climate change have resulted in several misapplications of the criteria (Akçakaya *et al.*, 2006). Extinction risk is often inferred from measures of change in range area (IUCN, 2010b), even though theory suggests it is unlikely that species' abundance will decline at the same rate as its distribution (Lawton, 1993; Gaston *et al.*, 2000). With the prospect of listing species that face imminent and significant range changes, and recognizing inherent difficulties of inferring extinction risk from predicted range change, the IUCN has recently recommended techniques be developed to better approximate threats to species' persistence from predicted range changes, with particular emphasis on the use of SDMs (IUCN, 2010a). One of the goals of the research presented here is to begin to examine how outputs from correlative SDMs can more reliably be used to assess taxa against the Red List criteria, using some well-studied case examples of plants from Australia.

To assess whether projected changes in extinction susceptibility are affected by explicitly considering species' population dynamics, we compare predictions of forecast changes in species range area and range margin movement derived from habitat models with and without coupled population models. We consider two types

of risk metrics: (i) indirect inferences of extinction proneness that can be estimated from correlative SDMs alone, i.e., measures of change in range area are used to infer extinction likelihood (Thomas *et al.*, 2004) and (ii) direct measures of extinction risk, which can only be estimated when stochastic-demographic models are part of the estimation method, i.e., expected minimum abundance (McCarthy & Thompson, 2001). We use five species to test the relative influence that the type of habitat suitability model, the climate change scenario and the various demographic factors have on inferred and measured extinction risk. By comparing projected habitat suitability, range area, and population abundance across species and climate scenarios, we examine whether demographic traits, either alone or in combination with habitat configuration, dictate whether range area estimates provide a reasonable approximation of abundance.

A second goal of this study is to address the issue of consistency in predictions of climate impacts on biodiversity. To date, debate has focused primarily on comparing the usefulness of different SDM techniques (e.g., Morin & Thuiller, 2009; Buckley, 2010; Kearney *et al.*, 2010). Here, we compare the suitability of using surrogates of extinction risk over targeted (and more difficult to estimate) measures of population viability, and the comparative value of range area estimates obtained from simple correlative approaches vs more ecologically-based approaches that explicitly account for demographic processes and habitat spatial structure.

Methods

Case study species

We identified appropriate plant species for this analysis, based on the following criteria: (i) the availability of representative point location data; (ii) an established understanding of the climatic and environmental conditions that define each species distribution; and (iii) strong knowledge of species' population dynamics (i.e., survival, recruitment and dispersal rates and how they respond to environmental variability and density feedbacks). Five Australian native plants, with contrasting life histories, were selected: *Angophora hispida, Banksia baxteri, Hakea constablei, Senecio macrocarpus* and *Xanthorrhoea resinosa*.

Location data

Occurrence records were extracted from surveys undertaken by Australian State Government agencies (Department of Environment and Natural Resources [http://www.environment.sa.gov.au/]; Office of Environment and Heritage [http://www.environment.nsw.gov.au/]; and Department of Sustainability and Environment [http://www.dse.vic.gov.au/dse/index.htm]). *Banksia* records came from the Banksia Atlas (see Yates *et al.*, 2010 for further details). All records were

scrutinized and any questionable points (in particular, those lying outside the present day distribution, as perceived by expert opinion) were removed. The number of unique occurrence records for each species was: *A. hispida* = 254; *B. baxteri* = 175; *H. constablei* = 109; *S. macrocarpus* = 95; and *X. resinosa* = 1140.

Climate and environmental spatial data

We identified four climate variables as being most relevant to plant survival and recruitment in southern Australia. These were: (i) maximum temperature in the warmest month; (ii) minimum temperature in the coolest month; (iii) summer rainfall; and (iv) winter rainfall. Meteorological weather station data was sourced for Australia from the Queensland Government SILO patched point database (http://www.longpaddock.qld.gov.au/silo/), which provides a comprehensive archive of Australian rainfall and temperature data. The archive is constructed from ground-based observational data, whereby continuous and complete daily time step records have been constructed using spatial interpolation algorithms to estimate missing data (Jeffrey *et al.*, 2001). Monthly daily temperature records [number of stations (ns) = 735] were averaged and rainfall (ns = 3060) measurements summed for the 20-year baseline period 1980–1999. Monthly values were averaged across years and across seasons (where applicable), producing mean estimates centred on 1990. The weather-station data were smoothed spatially using thin-plate-smoothing spline-fitting techniques (Hutchinson, 1995) in ANUSPLIN v4.36 (http://fennerschool.anu.edu.au/publications/software/anusplin.php), producing high resolution gridded climate surfaces (0.01° × 0.01° latitude/longitude; see Fordham *et al.*, 2012).

We generated an annual time series of climate-change layers for each variable according to two emission scenarios: a high CO_2 concentration stabilising reference scenario (WRE750) and a more conservative scenario that assumes substantive intervention (LEV1) (Wigley *et al.*, 1996, 2009). The procedure comprised two main parts (for further details see Fordham *et al.*, 2011a,b):

1 MAGICC/SCENGEN 5.3 (http://www.cgd.ucar.edu/cas/wigley/magicc), a coupled gas-cycle/aerosol/climate model, used for sensitivity analysis in the IPCC Fourth Assessment Report (IPCC, 2007), was employed to generate an annual time series of future climate anomalies (2000–2100) using an ensemble of nine GCMs, chosen on the basis of their skill in reproducing the Australian baseline climate (1980–1999), specifically: annual, winter and summer precipitation and temperature. The advantages of generating climate-model averaged ensemble forecasts have been recently reviewed (Fordham *et al.*, 2011a). Models were chosen using a number of comparison (or validation) metrics: (i) model bias (i.e., the difference between model and observed spatial means averaged over a user-specified area); (ii) pattern correlation; and (iii) standard and centred root-mean-square errors. Rather than using actual values of these various statistics, we placed them on a level playing field by using only model ranks for each statistic. Our key overall comparison metric is the cumulative rank (Fordham *et al.*, 2011a).

MAGGICC/SCENGEN also allows for an outlier analysis to be computed which compares future projections based on individual models with the average projection of all other models (Fordham *et al.*, 2011b). The nine GCMs used were GFDL-CM2.1, MIROC3.2(hires), ECHAM5/MPI-OM, CCSM3, ECHO-G, MRI-CGCM2.3.2, UKMO-HadCM3, GFDL-CM2.1, MIROC3.2(medres), where model terminology follows that used in the CMIP3 model data base (http://www.pcmdi.llnl.gov/ipcc/about_ipcc.php).

Although different skill ranking approaches might result in a different candidate set of skilful models, if the ensemble average is based on more than five GCMs, model choice has a reduced effect on the average forecast (Pierce *et al.*, 2009).

2 These climate anomalies were downscaled to an ecologically relevant spatial scale (0.01 × 0.01° longitude/latitude), using the 'change factor' empirical method, where the low-resolution change from a GCM is added to a high-resolution baseline observed climatology (Hulme *et al.*, 1995). Bi-linear interpolation of the GCM data (2.5 × 2.5°) to a finer resolution of 0.5 × 0.5° longitude/latitude was used to reduce discontinuities in the perturbed climate at the GCM grid box boundaries (Fordham *et al.*, 2011a, 2012). One advantage of this method is that, by using only GCM change data, it avoids possible errors due to biases in the GCMs baseline (present-day) climate.

Geological substrate has a large impact on plant distributions and persistence (Keith, 2011). We collapsed category classes in the Surface Geology of Australia dataset (1 : 1 million scale; Raymond & Retter, 2010) to generate binary suitable/not suitable maps on a per species basis. Because land clearing has exerted a strong historical effect on the distribution of many Australian species, we needed to mask predicted distributions to extant vegetation. We obtained the most recent Australia-wide gridded information on extant vegetation (NVIS data; http://www.environment.gov.au/erin/nvis/index.html) and updated it with newer data from New South Wales (Keith & Simpson, 2008). Post-prediction masks are available from the authors on request.

Species distribution modeling

We modeled the bioclimatic envelopes of all five species using an automated ensemble forecasting approach using a range of different techniques and a single forecasting technique implemented in consultation with experts on the species modeled.

The Bio-ensembles software (Diniz-Filho *et al.*, 2009) was used to generate climate envelopes using a large number of forecasts obtained from generating models with ten-fold cross-validated samples calibrated with 70% random subset of the data, six alternative combinations of variables (i.e., the full factorial combination of the four selected climatic variables), and seven bioclimatic-niche models (BIOCLIM, Mahalanobis and Euclidean distances, Generalized Linear Models, Random Forest, Maximum Entropy, and GARP). Models were calibrated using default options in Bio-ensembles (Diniz-Filho *et al.*, 2009). For models requiring records of absence as well as presence, pseudo-absences were chosen randomly from

locations with low climatic suitability (Wisz & Guisan, 2009), i.e., outside the observed 90th percentile for each climate variable. The number of pseudo-absences matched the number of presences. A habitat-suitability threshold was computed by extracting present-day Bio-ensemble suitability values for all presence location points and calculating the 5% quantile.

As an alternative, we used MaxEnt (Phillips *et al.*, 2006), with variable selection, iterative model fitting and evaluation undertaken in consultation with species experts (as opposed to using an automated full factorial combination of variables – the Bio-ensembles approach). MaxEnt adjusts choice of feature type and settings for complexity in relation to sample size. Software defaults were used except that threshold features were excluded (these tended to lead to overly complex fits). All presence records were used to fit the models. Background environments for MaxEnt models were constrained for four species, by taking background samples within biogeographic regions (IBRA v6.1; http://www.environment.gov.au/parks/nrs/science/bioregion-framework/ibra/) occupied by the species or neighboring these (Elith *et al.*, 2011 describe the rational for constraining background points). In contrast, the background environment for *B. baxterii* consisted of sites sampled for all banksias for a subregion of Western Australia, following Yates *et al.* (2010). The model results were assessed by experts for realism of the modeled relationships and the predicted current distributions. Thresholds of occurrence (Liu *et al.*, 2005) were based on quantiles of the occurrence records included in the final prediction; we explored 2.5%, 5% and 10% quantiles and found 5% gave results judged sensible by experts for all species.

Substrate is important in delimiting distributions of all these species, so we either: (i) ran climate-only models ('Bio-ensembles' and 'MaxEnt without substrate') and used substrate as a post-prediction mask (i.e., points on unsuitable substrates were assigned a habitat suitability value of zero); or (ii) included substrate as a predictor in the model (on the understanding that substrate and climate are together influencing the species' distribution in a potentially interactive way; the 'MaxEnt with substrate' model) and as a post-prediction mask. The geological mask was only used explicitly in the modeling process with MaxEnt because categorical variables cannot be handled by some of the models incorporated in the ensemble. In one region, substrate was highly correlated with summer rainfall, so for the species occupying that region (*H. constablei*) we dropped summer rainfall as a candidate variable for the climate plus substrate model on the understanding that the species is substrate-limited.

Overall, three correlative SDM runs (i.e., Bio-ensembles; MaxEnt with substrate; and MaxEnt without substrate) were used to forecast climate suitability in annual time steps (2000–2100) according to two emission scenarios (LEV1 and WRE750; see above).

Metapopulation modeling

We constructed spatially explicit stage-based stochastic matrix models for each species in RAMAS GIS v5 (Akçakaya & Root, 2005). All five of the case study species are hermaphroditic and

were modeled as females in RAMAS. A detailed description of the metapopulation models (including the stage structure of each cohort matrix population model) is provided in Appendix S1.

To determine the spatial structure of the metapopulation, we used an environmental-suitability layer consisting of the correlative SDM output, masked to exclude unsuitable substrates and areas cleared of native vegetation. Specifically, the distribution of suitable patches in each year (i.e., location, size, and shape) was determined based on a minimum habitat suitability threshold and a neighborhood distance (the spatial distance at which the species can be assumed to be panmictic). Suitable habitat was defined by the minimum threshold value obtained with correlative SDMs, representing the 10th percentile of non-zero habitat suitability values (see Appendix S1), for each cell in the modeled landscape. RAMAS GIS defined each patch in each annual correlative SDM for each species as a cluster of nearby grid cells with suitable habitat, and is assumed to support one population. Adjacent populations were delineated by a neighborhood distance threshold set to 1.5–2.0 km. The grid-cell clustering algorithm is described in Akçakaya & Root (2005).

Population models incorporated demographic and environmental variability, density dependence and dispersal. RAMAS GIS implements demographic stochasticity by sampling the number of survivors from binomial distributions, and the number of seeds produced from a Poisson distribution (Akçakaya & Root, 2005). Environmental stochasticity was sampled from lognormal distributions with coefficients of variation set to 10% for survival and growth transitions, and 20% for fecundity and germination transitions. To reduce likely truncations due to high survival rates, a negative correlation was imposed between the largest survival rate and other survival rates for each stage (Akçakaya & Root, 2005). Environmental variability was set to be correlated between populations depending on their spatial separation. Pairwise correlations were calculated using an exponential function, $P = a.exp(D^{c/b})$, where D is the distance between centroids of habitat patches and a, b and c are constants. We used regional variation in year-to-year annual rainfall to approximate environmental correlation for all species, other than $X. resinosa$, where winter rainfall was used. Similarly, Keith *et al.* (2008) used annual rainfall to approximate environmental spatial variability, because of it is role in governing rates of seedling establishment.

Density-dependence was implemented using a stage-structured model in which vital rates of the population were reduced whenever the density of the population exceeded a ceiling threshold (Keith *et al.*, 2008). Ceiling thresholds for each species were based on the mean area occupied by the canopy of a plant in the largest stage when unaffected by neighbors (i.e., maximum canopy size). Initially, the area of each habitat patch was divided by the maximum canopy size. This value was discounted by the mean proportion of mapped suitable habitat occupied by other plants species and unsuitable microhabitats to give the number of individuals in the largest-stage that could grow in the patch unconstrained by neighbors (i.e., the ceiling threshold). During simulations, the space used by the population in each patch was calculated by summing the number of individuals in each stage, multiplying these numbers by a stage-specific weight, and summing across all stages. Stage-specific weights were estimated from relative mean canopy areas of plants in each stage. For each time step, where the space used exceeded the ceiling threshold, rates of survival, growth and fecundity were reduced by a user-defined amount (see Appendix S1). This user-defined reduction increases linearly as the space used increases above the threshold. Seeds were excluded since they are not subject to density-dependent processes.

We modeled wildfires explicitly as catastrophes (similar to Keith *et al.*, 2008), with a mean fire return interval over 100 years of approximately 12 years, affecting vital rates (survival and fecundity) and density-dependent feedback processes in different ways depending on the species (see Appendix S1). For simplicity, we assume that fire frequency remains constant over the duration of the simulation. However, wildfires are expected to increase in frequency in response to climate change, though the severity of the shift remains uncertain (Williams *et al.*, 2009).

The probability of seed dispersal between patches of suitable habitat during each time step was modeled with an exponential function, $P = a.exp(D^{c/b})$, where D is the distance between patch centroids and a, b an c are constants. When D exceeds a specified maximum distance (D_{max}), P is set to zero. The parameters of the baseline dispersal model (suitable for $B. baxteri$, $H. constablei$ and $X. resinosa$) were adjusted to produce a shorter dispersal kernel for the passively dispersed $A. hispida$ and a longer dispersal kernel for the light-weight wind-dispersed $S. macrocarpus$ (see Appendix S1).

Initial abundance in the first time step (t) was firstly modeled as being equal to carrying capacity (i.e., the ceiling threshold). A period of 50–100 years (1000 permutations), depending on the life history of the plant, was then used to generate a stable age distribution and equilibrium initial patch abundance under the assumption of no future climate change. The initial abundance of patches located outside of suitable bioregions (as defined by the taxon-specific experts), which define present-day distribution (see above), were set to zero. Thus, these patches equate to areas that are climatically suitable, but not colonized, in the year 2000. Treating initial abundance as zero allows these areas of the range to be colonized in the future through demographic processes (such as dispersal) interacting with changes in habitat suitability.

Simulations

Patch structure was predicted for each species for each year between 2000 and 2100, using climate estimates from the future climate scenarios (WRE750 and LEV1, described above) and the selected species modeling methods. In these scenarios, species' spatial abundance patterns and range limits were driven by demographic processes, wildfires, climate change and the interaction between these. The stable climate scenario was modeled by keeping the climate envelope map for 2000 static throughout the simulation. Thus, under this scenario, only

demographic processes could cause changes in species distribution and abundance. All simulations were based on 10 000 stochastic replicates and run over a 101 year period (i.e., 2000–2100).

Proportional changes in a population viability metric, range margin movement and occupied range area were compared between 2020 and 2100, allowing sufficient time for the population to stabilise. More specifically:
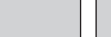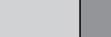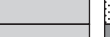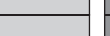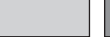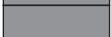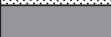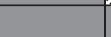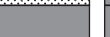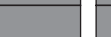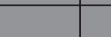
1 Population viability was assessed using expected minimum abundance (EMA; McCarthy & Thompson, 2001) in 2100, a continuous metric reflecting risks of both declines and extinction risk.

2 Range movement between 2020 and 2100 was calculated based on a weighted mean of the latitudes of the most northern/southern 10% of the metapopulation. Weights were the average population abundance of each patch in each year, and latitude was taken from the geographic center of the patch (Anderson *et al.*, 2009).
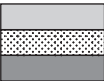
3 Changes in occupied range area (ORA) between 2020 and 2100 were investigated using the difference between the number of sites (~1 × 1 km latitude/longitude cells) gained by the species (i.e., sites where the species was present in 2100 but absent in 2020) and the number of sites lost (i.e., sites where the species was absent in 2100 but present in 2020) relative to the total number of sites occupied in 2100 (based on Buisson *et al.*, 2010). A density threshold value of one adult/km² was applied to spatial density maps. Thus, grid cells of very low adult abundance within a patch were considered unoccupied.

To compare estimates of suitability (and in turn occurrence) based on correlative SDMs with estimates from coupled

Table 1 Extinction risk metrics for five Australian plants according to different modeling approaches: (i) species distribution models only (SDM; range) and (ii) a coupled niche-population model (Niche-Pop Model; Range, EMA and North)

Species Name	SDM model	LEV1 SDM — Range	LEV1 Niche-Pop Model — Range	LEV1 Niche-Pop Model — EMA	LEV1 Niche-Pop Model — North	WRE750 SDM — Range	WRE750 Niche-Pop Model — Range	WRE750 Niche-Pop Model — EMA	WRE750 Niche-Pop Model — North
Angophora hispida	Bio-ensembles	▦	▦	▦	▦	■	■	■	▦
	MaxEnt	▦	▦	▦	░	░	░	■	▦
	MaxEnt (With Substrate)	▦	▦	▦	▦	░	░	■	▦
Banksia baxteri	Bio-ensembles	■	■	■	▦	■	■	■	▦
	MaxEnt	▦	▦	■	▦	■	■	■	▦
	MaxEnt (With Substrate)	■	■	■	▦	■	■	■	▦
Hakea constablei	Bio-ensembles	▦	▦	■	░	▦	▦	■	■
	MaxEnt	▦	▦	■	░	▦	▦	■	■
	MaxEnt (With Substrate)	■	■	■	░	■	■	■	▦
Senecio macrocarpus	Bio-ensembles	▦	▦	■	▦	▦	▦	■	▦
	MaxEnt	■	▦	■	▦	■	■	■	▦
	MaxEnt (With Substrate)	■	■	■	▦	■	■	■	▦
Xanthorrhoea resinosa	Bio-ensembles	▦	■	■	▦	▦	■	■	▦
	MaxEnt	■	▦	■	▦	■	■	■	░
	MaxEnt (With Substrate)	■	▦	■	▦	■	■	■	▦

Legend:
░ > 20%
▦ −20 to 20%
■ < −20%

Difference between the area of habitat gained and lost relative to predicted habitat area in 2020 according to species distribution models (SDM; Range) and differences in occupied area according to coupled niche-population models (Niche-Pop Model; Range). Also shown is the expected minimum adult abundance in 2100 relative to mean abundance in 2020 (EMA), and movement of the most northern 10th percentile of the metapopulation between 2020 and 2100 relative to the distance between the range margin and weighted population centroid in 2020 (Margin). Metrics are presented for three SDM approaches [Bio-ensembles, MaxEnt, MaxEnt (with substrate)] and two climate change scenarios: a high CO_2 concentration stabilising scenario (WRE750) and a heavy mitigation scenario, assuming substantive policy intervention (LEV1). See Methods for details.

niche-population models (i.e., correlative SDMs coupled with population models), changes in range area were similarly calculated for correlative SDM outputs. In this case, a habitat-suitability threshold, specific for each species and correlative SDM (see above), was used to distinguish between potentially occupied and unoccupied sites.

Detecting trends

General linear mixed-effects models (GLMM; Gaussian-identity distribution-link) were used to identify key determinants of expected minimum abundance ($n = 45$) and northern range margin movement ($n = 45$). Using monotonic or quadratic relations to normalize expected minimum abundance proved unsuccessful: a quantile-based approach was used to achieve normality (Jongman *et al.*, 1987). Likelihood ratio tests for mixed-effects models (Crainiceanu & Ruppert 2004) confirmed that plant species (*species*) should be treated as a random effect. Thus, models were not simplified to general least squares models (Pinheiro & Bates, 2000). Model fixed effects were: future climate scenario (*scenario*), modeling technique (i.e., uncoupled SDM or coupled niche-population model; *coupling*) and SDM approach (*approach*); area of suitable habitat in 2020 (*range*), the ratio between predicted number of patches and range size in 2020 (*patch.structure*).

We used general linear models (GLM; Gaussian-identity distribution-link) to explore the relative importance of different species specific traits on expected minimum abundance and northern range margin movement. These species traits were: maximum rate of population growth (*rmax*; low, medium or high); average dispersal distance for one in every 1000 individuals (*disp*); and recruitment response to *fire* (strong or weak).

We also investigated potential drivers of occupied range area ($n = 60$) in 2100 using GLMs (the response variable was scaled between 0 and 1 for each species). GLMs were used because likelihood ratio tests indicated a lack of support for treating *species* as a random factor. In each case, model residuals were inspected to confirm normality (Crawley, 2002). All GLMMs were fitted using the lmer function of the lme4 package in the *R* statistical package (v. 2.12.1; R Development Core Team 2010).

Results

Range Area: There was broad agreement in change in range area forecast for 2020 to 2100, regardless of whether the metric was predicted using uncoupled correlative SDMs or coupled niche-population model (Table 1) – the former being based on habitat suitability above a SDM/species specific threshold, the latter on estimates of occupied range area. However, the choice of underlying habitat model (SDM approach) largely influenced the extent and, in some instances, the direction (Table 1) of change in occupied range area between 2020 and 2100 (e.g., Figs 1 and 2). Consistent with previous studies, the GLM analysis indicated that SDMs
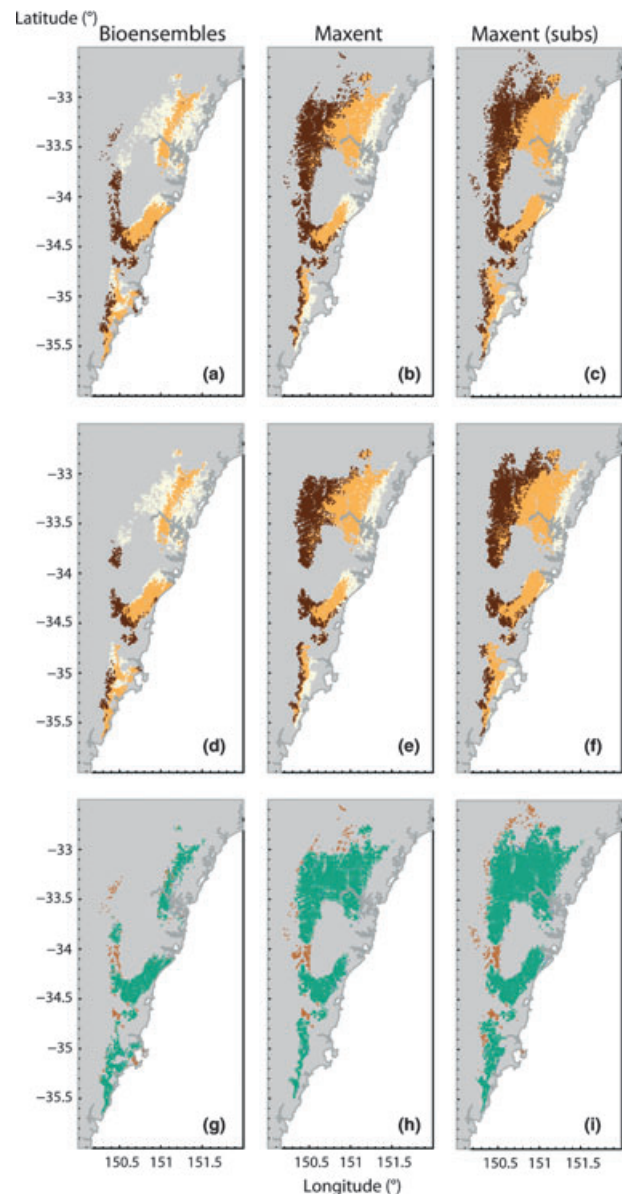
Fig. 1 Impact of species distribution modeling approach [Bioensembles; MaxEnt; MaxEnt (with substrate)] on the area and location of suitable habitat or occupied habitat maintained (orange), lost (yellow) and gained (red) between 2020 and 2100 for the Australian shrub *Angophora hispida* according to uncoupled species distribution models (a–b) and coupled niche-population models (d–f). The climate is assumed to follow a high CO_2 concentration stabilising scenario (WRE750). Congruence between coupled and uncoupled modeling approaches for forecast occurrence (green) of *A.hispida* in 2100 is mapped (g–i). Suitable areas according to only the uncoupled distribution modeling approach are also mapped (brown). There were very few cells suitable according to only the coupled niche-population model.

(*approach*) contributed more variability in estimates of change in range area than did either climate change scenario, and here we found this was true also when
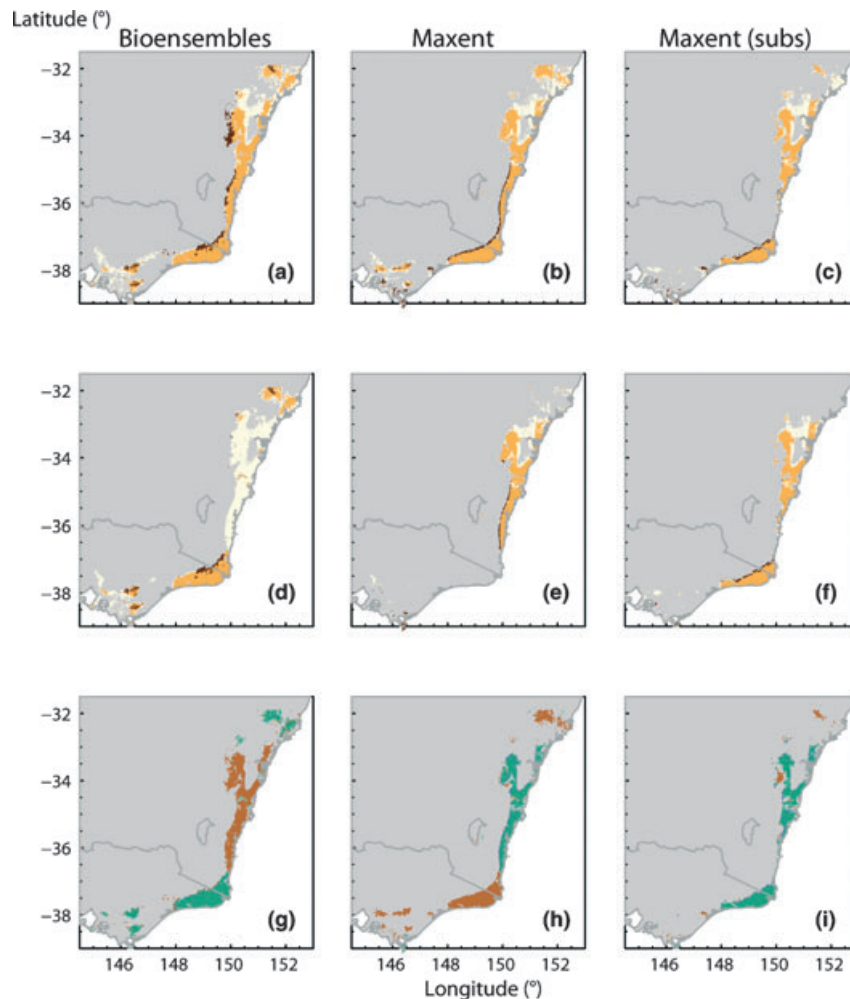
Fig. 2 Impact of species distribution modeling approach [Bioensembles; MaxEnt; MaxEnt (with substrate)] on the area and location of suitable habitat maintained (orange), lost (yellow) and gained (red) between 2020 and 2100 for the Australian grasstree *Xanthorrhoea resinosa* according to uncoupled species distribution models (a–b) and coupled niche-population models (d–f). The climate is assumed to follow a high CO_2 concentration stabilising scenario (WRE750). Congruence between coupled and uncoupled modeling approaches for forecast occurrence (green) of *X. resinosa* in 2100 is mapped (g–i). Suitable areas according to only the uncoupled distribution modeling approach are also mapped (brown). There were few cells suitable according to only the coupled niche-population model.

correlative SDMs were coupled to population models (*coupling*) (Table 2; Appendix S2). Although AIC support for the two top-ranked models was nearly equal (*approach + coupling*; $w_i = 0.38$); (*approach*; $w_i = 0.31$; $\Delta AICc = 0.38$), the majority of deviance in estimated range area was explained by the single parameter *approach*-only model (~56% vs 66%).

Accordingly, the area and spatial pattern of suitable habitat (according to uncoupled models) and occupied habitat (according to coupled models) were quite similar for a given correlative SDM run (Fig. 1, comparison within columns). However, for some species and correlative SDM approach, differences in forecast suitability and occupied habitat were apparent (e.g., Fig. 2, see areas mapped brown in bottom row). In

some instances, the explicit inclusion of substrate in the habitat sub-model resulted in more constrained range area projections. For example, the disjunction in the distribution of *X. resinosa* on the south coast was only captured by the MaxEnt approach that included geological substrate in the model (Fig. 2, right column).

Expected Minimum Abundance: Trends in expected minimum abundance (a direct measure of extinction risk) were not consistent with area-type surrogates of extinction threat (Table 1). The contrast was most notable for the LEV1 emission scenario, which assumes substantive human intervention to reduce climate change, and presumably a slower rate of change in habitat suitability. In contrast to estimated range area, there was

Table 2 Summary set of general linear models for predicted range area in 2100 (dependent variable) according to habitat-only models and models with both population and habitat dynamics

Model	k	LL	ΔAIC_c	$wAIC_c$	%DE
approach + coupling	3	−4.13	0	0.38	66.4
approach	2	−5.47	0.38	0.31	55.6
approach + scenario	3	−5.31	2.36	0.12	56.9
coupling	2	−11.25	11.94	0	8.6
scenario	2	−12.18	13.80	0	1.0

Number of parameters (k), log likelihood (LL), change in AIC_c compared to the best-ranked model (ΔAIC_c), AIC_c model weights ($wAIC_c$), and the percentage of explained deviance (% DE) for the response variable, range area in 2100 proportional to maximum range area per species. Range area is based on habitat suitability for habitat only models and occupied range area for models that couple population dynamics and habitat (see Methods for further details). Fixed effects (predictors) include climate scenario (*scenario*), modeling technique [i.e., uncoupled species distribution model (SDM) or coupled niche-population model model; *coupling*] and SDM approach (*approach*). See Appendix 2 for the complete general linear model set.

no support for the hypothesis that the explanatory variable *approach* (type of correlative SDM) has a strong influence on expected minimum abundance (Table 3, Appendix S3). Rather, the ratio between predicted number of patches and range size in 2020 was the best predictor of expected minimum abundance (*patch.range* + [1 | *species*]; $w_i = 0.91$). However, a large proportion of the observed deviance (69% vs 72%) was explained by the second-ranked model, which included only the taxonomic random effect (*1* + [1 | *species*]; $w_i = 0.02$; $\Delta AICc = 7.96$).

Adopting a simplified GLM framework, and substituting the random effect with key population traits, showed a greater level of support for fire-based recruitment rates (compared to dispersal and population growth rate) as the most parsimonious demographic predictor of EMA (*fire*; $w_i = 1$) for the five plant species, explaining ~58% of the structural deviance (Table 4).

Range Margin Movement: Range margins for most of the Australian plant species under analysis were predicted to experience large shifts between 2020 and 2100 (Appendix S4), especially those at the northern boundary (Fig. 3, Appendix S5). Although climate scenario and correlative SDMs influenced the speed and direction of annual predicted movement of the most northern 10% of the metapopulation (Fig. 3), patch structure (*patch.range* + [1 | *species*]; $w_i = 0.539$) had the strongest influence on northern range margin movement between 2020 and 2100 (Table 3, Appendix S3). There was also reasonable support for the next-ranked models: the null, *1* + [1 | *species*] ($w_i = 0.15$; $\Delta AIC_c = 2.6$); and *scenario* + [1 | *species*] ($w_i = 0.13$; $\Delta AIC_c = 2.85$). Again, the random effect accounted for the largest proportion of the deviance explained (~11% compared to 14% for the AIC_c best model).

Unlike expected minimum abundance, there was little support that fire tolerance influenced northern range margin movement (i.e., unable to detect the influence of fire tolerance on extinction risk). Instead, modeling northern range movement as a function of dispersal had the strongest AIC_c support (*dispersal*; $w_i = 0.44$; Table 4). Although there was similar support for a more parameter rich model, with dispersal and its interaction with patch structure (*patch.range:dispersal*; $w_i = 0.40$; $\Delta AIC_c = 0.21$), the single parameter dispersal

Table 3 Summary set of general linear mixed effects models for expected minimum abundance (EMA) and movement of the northern range margin (Margin) as the dependent variables

Response	Model	k	LL	ΔAIC_c	$wAIC$	%DE
EMA	*patch.structure*+(1 | *species*)	4	−34.08	0.00	0.96	72.9
	1+(1 | *species*)	3	−39.27	7.96	0.02	68.8
	scenario+(1 | *species*)	5	−38.96	12.30	0.00	69.0
	approach+(1 | *species*)	5	−40.20	14.77	0.00	68.0
Margin	*patch.structure*+(1 | *species*)	4	−73.99	0.00	0.54	13.5
	1+(1 | *species*)	3	−76.48	2.56	0.15	10.6
	scenario+(1 | *species*)	5	−74.15	2.85	0.13	13.3
	approach+(1 | *species*)	5	−76.01	6.58	0.02	11.1

Number of parameters (k), log likelihood (LL), change in AIC_c compared to the best-ranked model (ΔAIC_c), model weights ($wAIC_c$) and percentage explained deviance (%DE), for two separate general linear mixed effects model sets. The response (or dependent) variables for these different model sets were: (i) expected minimum abundance in 2100 (EMA); and (ii) movement of the northern most 10% of the population between 2020 and 2100 relative to maximum movement recorded across species and scenarios (Margin). Fixed effects (predictors) included: future climate scenario (*scenario*), species distribution modeling approach (*approach*) and the ratio between predicted number of patches and range size in 2020 (*patch.structure*). *Species* was treated as a random effect. See Appendix 3 for the complete general linear mixed effects model set.

Table 4 Relative influence of spatial structure and key population traits on expected minimum abundance and movement of the northern range margin

Response	Model	k	LL	ΔAIC_c	$wAIC_c$	%DE
EMA	*fire*	2	−50.24	0.00	1	57.6
	rmax	3	−61.11	24.15	0	31.3
	dispersal	2	−64.66	28.84	0	19.6
	patch.structure+dispersal	3	−64.53	30.99	0	20.0
	patch.structure:dispersal	4	−64.53	33.52	0	20.1
	null	1	−69.56	36.34	0	0.0
	patch.structure	2	−69.37	38.25	0	0.9
Margin	*dispersal*	2	−76.40	0.00	0.44	33.4
	patch.structure:dispersal	4	−74.03	0.21	0.40	40.0
	patch.structure+dispersal	3	−76.25	2.11	0.15	33.8
	fire	2	−82.34	11.88	0	13.3
	patch.structure	2	−84.15	15.50	0	6.0
	null	1	−85.54	15.98	0	0.0
	rmax	3	−85.24	20.10	0	1.3

Number of parameters (k), log likelihood (LL), change in AIC_c compared to the best-ranked model (ΔAIC_c), model weights ($wAIC_c$) and percentage explained deviance (%DE) for two separate general linear model sets. The response (or dependent) variables for these different model sets were: (i) expected minimum abundance in 2100 (EMA); and (ii) movement of the northern most 10% of the population between 2020 and 2100 relative to maximum movement recorded across species and scenarios (Margin). Predictor variables included: maximum rate of population growth (*rmax*; low, medium or high); average dispersal distance for one in every 1000 individuals (*disp*); recruitment response to *fire* (strong or weak); and the ratio between the predicted number of patches and range size in 2020 (*patch.range*). The null model (*null*) assumes a single rate across species, scenario and method. See Methods for further details.

model explained the majority of structural deviance (33% vs 40% for the more parameterized model).

Area and population size

Relative change in summed habitat suitability tended to track occupied range area across species and climate scenarios (Fig. 4; Appendix S6). However, the relationship between relative change in population size and measures of range area differed between species and scenarios of habitat change (the result of emission scenario and correlative SDM approach). In some cases, populations declined more or less linearly with total habitat suitability and occupied range area (Fig. 4). However, for the majority of species and scenarios, the relationship was strongly non-linear (Fig. 4; Appendix S6). In fact, in some cases population size actually increased despite a persistent decline in total habitat suitability and occupied range area (Fig. 4), most likely caused by an increase in density in highly suitable areas due to non-equilibrium density dependence.

Discussion

For five species of Australian plants with contrasting demographic traits, our results demonstrate that the relationship between relative change in range area and population abundance is rarely linear and sometimes inverse, differing between species and amongst scenarios of projections of habitat change within a species. Our simulations reveal that direct measures of climate-induced extinction risk and demographic-based range-margin movement are strongly affected by key demographic traits, but not variation between temporal patterns of spatial habitat suitability (which can result from different correlative SDM approaches). Moreover, commonly used proxies of climate-driven extinction risk (e.g., measured change in range area) were found to be most sensitive to the habitat suitability model. These results underscore the need to consider direct measures of extinction risk (population viability), as well as measures of change in habitat area, when assessing climate change impacts on biodiversity. Our results, therefore, provide additional support for using sophisticated methods, where data permit, that couple spatial environmental variability with population dynamics: a technique that has gained support on theoretical grounds (Huntley *et al.*, 2010).

Methods used to predict species distributions affect predictions both for baseline conditions (Elith *et al.*, 2006), and for forecasting changes under climate change (Araújo & Rahbek, 2006; Elith *et al.*, 2010). The
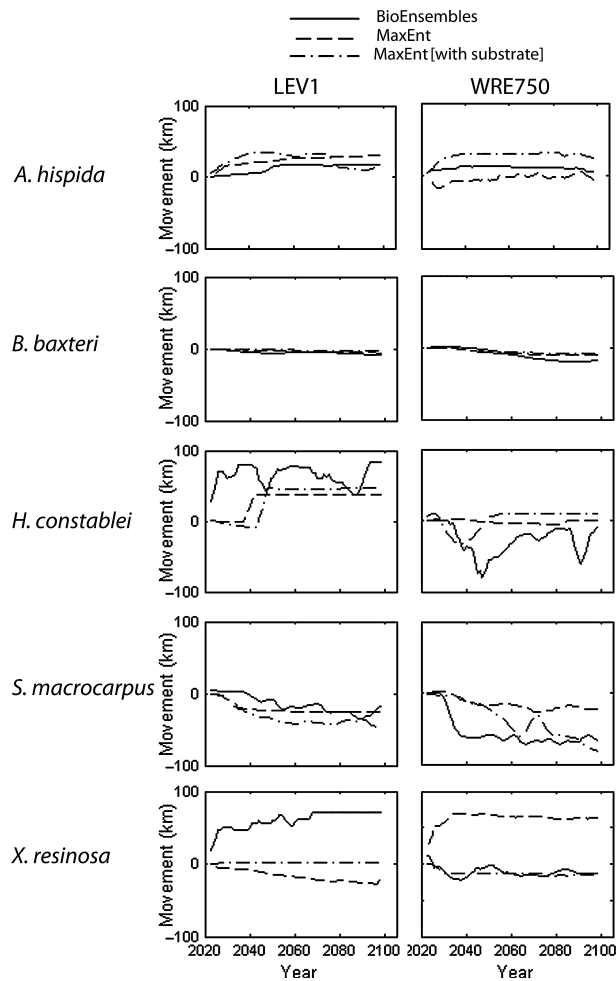
Fig. 3 Range movement in the most northern 10 per cent of the metapopulation for *Angophora hispida, Banksia baxteri, Hakea constablei, Senecio macrocarpus* and *Xanthorrhoea resinosa* between 2020 and 2100, according to three different species distribution modeling approaches [Bio-ensembles, MaxEnt, MaxEnt (with substrate)] and two climate change scenarios (LEV1; WRE750). See Methods for details.

latter typically culminates in considerable model disagreement (Pearson *et al.*, 2006). In this study, we have shown that the approach used for fitting SDMs strongly influences projected changes in range area and spatial patterns of abundance in the coupled niche-population model. That is, the area and spatial pattern of suitable and occupied habitat, according to coupled and uncoupled models respectively, was quite similar for a given SDM technique. This important observation indicates that the effect of the SDM carries through to the coupled model. Thus, SDM model uncertainty must be considered in any management decision that uses occupied range area to evaluate extinction proneness. For example, quantifying variance components can be used

to evaluate variability in SDM-based recommendations for conservation practitioners (Mbogga *et al.*, 2010).

Factors that regulate a species' geographic extent and spatial abundance, operating singly or in combination, ultimately influence vital rates (survival and reproduction) and associated population traits (Gaston, 2003). Range margins occur where individual populations are no longer sustained by local recruitment or dispersal from adjacent areas, because local deaths exceed local births and immigrations (Caughley *et al.*, 1988). Thus, it is interesting that our occupied range area estimates for five plant species tended not to be heavily affected by the explicit modeling of population dynamics. Yet, in line with our hypothesis, key life-history traits and, to a lesser degree, landscape spatial structure, had a strong influence on expected minimum abundance (a direct measure of extinction risk) and on a metric of range margin movement. Fire tolerance had the largest influence on expected minimum abundance, while long-distance dispersal rate and its interaction with the spatial configuration of the landscape in 2020, had the strongest effect on northern range margin movement.

Projected abundance did not typically respond linearly to changes in summed habitat suitability and geographic extent for the five plant species, which is to be expected since population persistence was sensitive to different drivers of variation than habitat area. However, this observation has important ramifications for the use of habitat-area-change metrics as proxies for extinction risk. The key issue is that inferring extinction risk from projected changes in geographic extent is constrained by an underlying assumption of a linear relationship between abundance and range area. Although this relationship is usually positive, the relationship may have multiple forms (Blackburn *et al.*, 2006), meaning that it is unlikely that species' abundance will decline at the same rate as its range area (Lawton, 1993). This assumption is especially problematic in the context of climate change because several additional factors are likely to exacerbate the climatic effects on species persistence beyond the effects predicted by changes in available habitat area (Botkin *et al.*, 2007).

Although the relationship between the relative change in summed habitat suitability, range area and population size differed between species and across scenarios of habitat change within species, the relationships revealed in our simulations were rarely linear (Fig. 4). For example, the population density of *S. macrocarpus* increased heavily between 2020 and 2100, while habitat suitability and occupied range area only changed marginally, causing average cell density to increase. In the case of *H. constablei*, population density remained high (in some cases increasing) despite a
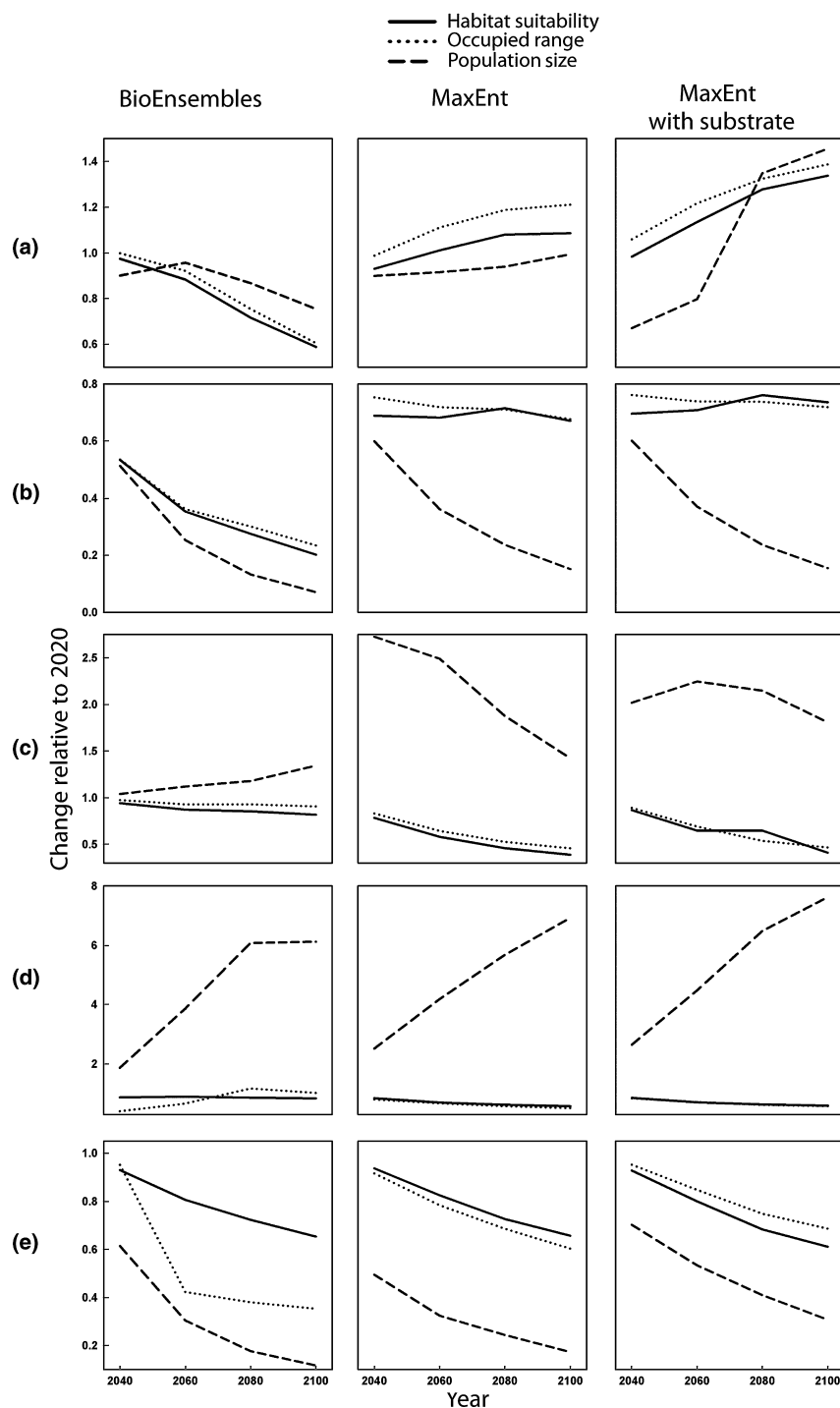
Fig. 4 Change in summed habitat suitability, occupied range area and population size between 2020 and 2100 for *Angophora hispida* (A), *Banksia baxteri* (B), *Hakea constablei* (C), *Senecio macrocarpus* (D) and *Xanthorrhoea resinosa* (E) according to three different species distribution modeling approaches [Bio-ensembles, MaxEnt with and without non-climate parameters (substrate)] and a high CO_2 concentration stabilising scenario (WRE750

gradual decrease in habitat suitability and range area. We suspect that these nonlinearities are caused by a combination of weak density dependence (which results in weak coupling of habitat change and population dynamics; see below) and highly variable population dynamics driven by complex interactions between

fire and demography. For *A. hispida*, the relationship between habitat area and population size differed between climate scenario as well as SDM approach, highlighting further the importance of suitable habitat structure and area, as well as demographic traits, in defining the connection between abundance and range area.

Our application of the coupled niche-population modeling approach simulated the effects of climate change only through its impact on the species' habitat. For species with a strong linkage between habitat and vital rates (i.e., for species with moderate to strong density dependence) the effect on habitat translates to effects on vital rates, so there is an indirect effect of climate change on vital rates. In principle, direct effects of climate change on vital rates can also be incorporated in this framework. For instance, Keith *et al.* (2008) used the same linked habitat-demographic approach to incorporate direct effects of climate change on plant fecundity through changes in fire regimes. However, in our application, data were not available on the relationship between fire and fecundity for all species. One result is that for species with weak density-dependence, the linkage between habitat and demography is weak and thus, the effects of climate change are likely to be underestimated. This is probably one of the reasons why, for *H. constablei* and *S. macrocarpus*, habitat and viability change in opposite directions. This observation demonstrates that in order to correctly assess the effects of climate change within this framework, the effects of climate on demography (either direct or indirect) must be fully accounted for.

To overcome problems with inferring population decline from projected changes in habitat suitability derived from correlative SDMs, the IUCN has suggested using a minimum habitat suitability threshold to exclude areas unlikely to be suitable and removing fragments that are too small and isolated to support viable populations (IUCN, 2010a). Although, such measures may be appropriate in instances where deteriorating suitability and range area is associated with a decline in population size, they will do little to strengthen confidence in range-area type proxies of extinction risk if population abundance is expected to increase despite a contraction in range area; or where the rate of change in abundance strongly outpaces changes in total habitat suitability. Nonlinearities such as these were observed among the five Australian plant species, making declines in habitat area crude and sometimes misleading proxies of extinction risk. Thus, results from distribution and demographic modeling techniques, which assume that extinction risk is inversely related to range or habitat patch area (e.g., Wilson *et al.*, 2010), should be interpreted cautiously.

Our research on Australian plants strengthens the argument for continuing to develop and link correlative SDMs with metapopulation models because habitat-demographic approaches provide direct measures of extinction risk, in addition to range area type proxies of extinction threat. In doing so, they will be able to offer more appropriate conservation measures to offset climate change impacts. However, these techniques are data intensive, requiring a strong understanding of the population dynamics of the focal species (as well as distributional data), so they will not be possible for the majority of the world's species.

A potential solution is to use these more sophisticated methods selectively, through a targeted approach aimed at developing general guidelines that better describe traits and conditions that make some species more vulnerable to climate change than others (Akçakaya *et al.*, 2006; Brook *et al.*, 2009). Building spatially explicit population models with dynamic landscape structure for a wide range of 'exemplar taxa' with contrasting life histories (such as dispersal ability, generation time, rate of population growth) will enable (i) a more appropriate weighting of climate-change impacts against other drivers of biodiversity loss, and (ii) a quantitative determination of how climate change will act synergistically with existing threats such as land use change and habitat fragmentation. Sensitivity analyses should be an important component of such comparative work, as it will help in establishing the life-history characteristics under which the effects of climate change on species viability are exacerbated beyond the effects predicted by change in available habitat area.

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Supporting Information

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

Appendix S1. Detailed description of demographic models.
Appendix S2. Complete set of general linear models for predicted range area in 2100 (dependent variable) according to habitat-only models and models with both population and habitat dynamics.
Appendix S3. Complete set of general linear mixed effects models for expected minimum abundance in 2100 and movement of the northern range margin between 2020 and 2100 (as the dependent variables).
Appendix S4. Absolute distance forecasts of range movement for five plant species between 2020 and 2100 in response to three climate scenarios and three SDM approaches.
Appendix S5. Range movement in the most southern 10 per cent of the metapopulation for *Angophora hispida, Banksia baxteri, Hakea constablei, Senecio macrocarpus* and *Xanthorrhoea resinosa* between 2020 and 2100, according to three different SDMs [Bio-ensembles, MaxEnt, MaxEnt (with substrate)] and two climate change scenarios (LEV1; WRE750). See Methods for details.
Appendix S6. Change in summed habitat suitability, occupied range area and population size between 2020 and 2100 for *Angophora hispida*(A), *Banksia baxteri*(B), *Hakea constablei* (C), *Seneciomacrocarpus* (D) and *Xanthorrhoea resinosa* (E) according tothree different species distribution modeling approaches [Bio-ensembles, MaxEnt with and without non-climate parameters (substrate)] and a low CO_2 concentration stabilising scenario (LEV1).

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