

# Impact of landscape predictors on climate change modelling of species distributions: a case study with *Eucalyptus fastigata* in southern New South Wales, Australia

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## ABSTRACT

**Aim** We consider three questions. (1) How different are the predicted distribution maps when climate-only and climate-plus-terrain models are developed from high-resolution data? (2) What are the implications of differences between the models when predicting future distributions under climate change scenarios, particularly for climate-only models at coarse resolution? (3) Does the use of high-resolution data and climate-plus-terrain models predict an increase in the number of local refugia?

**Location** South-eastern New South Wales, Australia.

**Methods** We developed two species distribution models for *Eucalyptus fastigata* under current climate conditions using generalized additive modelling. One used only climate variables as predictors (mean annual temperature, mean annual rainfall, mean summer rainfall); the other used both climate and landscape (June daily radiation, topographic position, lithology, nutrients) variables as predictors. Predictions of the distribution under current climate and climate change were then made for both models at a pixel resolution of 100 m.

**Results** The model using climate and landscape variables as predictors explained a significantly greater proportion of the deviance than the climate-only model. Inclusion of landscape variables resulted in the prediction of much larger areas of existing optimal habitat. An overlay of predicted future climate on the current climate space indicated that extrapolation of the statistical models was not occurring and models were therefore more robust. Under climate change, landscape-defined refugia persisted in areas where the climate-only model predicted major declines. In areas where expansion was predicted, the increase in optimal habitat was always greater with landscape predictors. Recognition of extensive optimal habitat conditions and potential refugia was dependent on the use of high-resolution landscape data.

**Main conclusions** Using only climate variables as predictors for assessing species responses to climate change ignores the accepted conceptual model of plant species distribution. Explicit statements justifying the selection of predictors based on ecological principles are needed. Models using only climate variables overestimate range reduction under climate change and fail to predict potential refugia. Fine-scale-resolution data are required to capture important climate/landscape interactions. Extrapolation of statistical models to regions in climate space outside the region where they were fitted is risky.

## Keywords

Australia, climate change, climate envelope modelling, *Eucalyptus*, generalized additive modelling, realized niche, refugia, solar radiation, species distribution modelling.

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## INTRODUCTION

Statistical species distribution models (SDMs) are increasingly used to predict the potential changes in species distributions under climate change (Elith & Leathwick, 2009). There is, however, increasing concern about the assumptions and approaches being adopted in these studies (Araújo & Luoto, 2007; Beale *et al.*, 2008; Jeschke & Strayer, 2008; Luoto & Heikkinen, 2008; Morin & Lechowicz, 2008; Pöyry *et al.*, 2008; Randin *et al.*, 2009; Willis & Bhagwat, 2009). Of particular concern are: (1) the assumption that, for studies of a large area (extent), climate variables alone are sufficient predictors (e.g. Araújo & Guisan, 2006, pp. 1681–1682); (2) the assumption that a spatial resolution for species distribution modelling at  $10 \times 10$  km or  $50 \times 50$  km pixels is appropriate and does not lead to biased models (e.g. Huntley *et al.*, 2004; Araújo *et al.*, 2006; Luoto *et al.*, 2006; Thuiller *et al.*, 2006; Pöyry *et al.*, 2008; Svenning *et al.*, 2008); and (3) the fact that where non-climatic variables have been included in species distribution modelling there is no consistency in the number of variables nor in which variables are selected, making comparisons difficult (e.g. Iverson *et al.*, 2008; Keith *et al.*, 2008; Randin *et al.*, 2009). In our companion paper (Austin & Van Niel, 2010), we suggested that adopting a simple conceptual framework of the potential ecological variables will facilitate the testing of ecological assumptions implicit in SDMs, and the comparison of alternative predictors for the same biophysical process, while providing criteria for deciding on the scale of resolution. We used the example of solar radiation as an environmental predictor for the role of light. Ecological knowledge of the effect of radiation indicates that the greatest differences will occur as a result of aspect and local topography, which will be recognized only at a resolution of less than 100 m. The resulting differences could be equivalent to shifts of 200 km north or south. The implication is that local refugia may not be detected if coarse-scale data are used for modelling.

Here we present a case study using light (incident solar radiation) to examine the following three questions. (1) How different are the predicted distribution maps when climate-only and climate-plus-terrain models are developed from high-resolution data? (2) What are the implications of differences between the models when predicting future distributions under climate change scenarios, particularly for climate-only models at coarse resolution? (3) Does the use of high-resolution data and climate-plus-terrain models predict an increase in the number of local refugia? We use simple landscape predictors within an explicit, conceptual framework to model species distributions using a minimally complex statistical method. If a single species can be shown to require local landscape predictors for effective modelling, and these additional predictors result in alternative interpretations of the outcome of climate change, then the performance of very low-resolution SDMs needs to be calibrated with high-resolution data before conclusions are drawn on future changes in distributions based on low-resolution climate-only models.

## MATERIALS AND METHODS

### Conceptual framework

Plant growth and distribution are conventionally presented as being controlled by both environmental and biological variables:

$$\begin{aligned} \text{Species abundance} \\ = f(\text{light, temperature, nutrients, water, CO}_2, \text{disturbance, biota}). \end{aligned} \quad (1)$$

These variables summarize the necessary inputs for plant survival and reproduction plus disturbance and biotic interactions. The equation does not specify whether light should be expressed as a photoperiod or a seasonal radiation measure for the purpose of modelling. This is a matter for study when developing an SDM. We suggest the use of equation 1 as a checklist to justify explicitly and consistently the selection of environmental predictors [and see Austin & Van Niel (2010) for a table demonstrating the varied use of both climatic and non-climatic variables].

### Study area

Parts of our study area and data have previously been used extensively for modelling *Eucalyptus* species distributions (e.g. Austin *et al.*, 1990, 1997; Austin, 1992; Van Niel & Austin, 2007). The current study area, in the south-eastern corner of New South Wales, Australia, south-east of a line running from Wollongong in the north to Albury, Victoria, on the southern border and east to the coast, is an expanded area compared with that used by Austin *et al.* (1990). Elevation varies from sea level to 2228 m on Mt Kosciuszko, Australia's highest point. Mean annual precipitation ranges from 480 mm to greater than 2100 mm, with marked seasonal differences in summer and winter. The mean daily temperature extremes are a minimum of 2.6 °C and a maximum of 17.2 °C. Precipitation and temperature figures were calculated from ANUSPLIN surfaces (Hutchinson, 1991).

### Data

The species data consist of the presence/absence of a single species, *Eucalyptus fastigata* Deane & Maiden, for 10,577 plots of specified size and location, together with environmental data for climate and local topography drawn from the *Biograd* database (E.M. Cawsey, CSIRO unpublished report).

*Eucalyptus fastigata* was chosen because previous analyses had indicated that the species was sensitive to radiation and topography (Austin, 1992, 1998). The vegetation plot data were collated from various sources based on minimum data set criteria. Only tree and shrub species capable of reaching the canopy were included. All plots had a specified size (0.04 to 0.4 ha) and location, allowing environmental variables to be estimated from Geographic Information Systems (GIS) or maps. The pixel resolution for all GIS data was 100 m, and the plot location error was less than 200 m.

The climate variables for rainfall and temperature were estimated for the plots and as GIS layers using location and elevation with ANUSPLIN climate surfaces for Australia (Hutchinson, 1991) and the ESOCIM module of the ANUCLIM software (Hutchinson *et al.*, 1999). Other local predictors, namely topographic position, lithology, slope and aspect, were derived either from a digital elevation model or from maps (CSIRO Division of Wildlife and Ecology, 1996).

## Selection of predictors

### 1. Light

Differences in solar radiation resulting from differences in aspect and slope have been shown to be important in modelling the realized niche of eucalypt species (Austin *et al.*, 1990, 1997). We use the ESOCIM module in ANUCLIM (Hutchinson *et al.*, 1999) to estimate actual radiation, including both direct and diffuse radiation and adjusting for slope and aspect, using sunshine hours and vapour pressure with 'ratio tables' of radiation for inclined versus flat surfaces based on values for three climate stations, namely Green Cape (150.05° E, 37.26° S), Nimmitabel (149.28° E, 36.52° S) and Kioloa (150.37° E, 35.55° S), which are representative of the regional variation in the study area. Horizon effects blocking radiation are not included. This procedure captures regional variation in radiation as well as topographic effects for average conditions. Mean daily radiation and June daily radiation are highly correlated ( $r = 0.898$ ). June radiation (WinRad) has a finer discrimination between plots, with a threefold difference between minimum and maximum observed values, compared with the twofold difference for mean daily radiation; it was therefore chosen to represent the light predictor.

### 2. Temperature

Mean annual daily temperature (MAT) has been found to be the most important predictor of eucalypt species distribution in a number of studies (e.g. Austin *et al.*, 1997). Mean daily temperature is correlated with maximum summer temperature ( $r = 0.734$ ) and highly correlated with July minimum temperature ( $r = 0.900$ ). Use of MAT was therefore continued as the sole predictor for temperature to avoid problems of collinearity between predictors. No transformation to growing degree-days (GDD) was made, as it is known that there is a very close relationship between GDD and MAT in this region of Australia ( $r > 0.98$ , Pausas *et al.*, 1997). In the absence of a suitable biophysical process model, the influence of local landscape differences in temperature was assumed to be captured by the local predictors WinRad and topographic position.

### 3. Water

No attempt was made to develop a moisture stress index as a proximal predictor for the water variable, as there was

insufficient information on soil properties or landscape position to estimate soil water storage for all plots. However, it is known that such an index, when based on soil survey data, is an important predictor of eucalypt stem density in the study area (Austin *et al.*, 1997). Precipitation was selected as a distal resource predictor for water supply. There is strong rainfall seasonality in the study area, so both mean annual rainfall (MAR) and mean summer rainfall (MSR) were included in the models because their correlation is weak ( $r = 0.569$ ). However, MAR is strongly correlated with mean winter rainfall ( $r = 0.796$ ), so winter rainfall was not included in the models.

### 4. Nutrients

No chemical data on soil nutrient concentrations were available. Expert opinion was therefore used as a distal surrogate predictor. The assessments were made on the basis of geological stratigraphic maps and analyses of total phosphorus for certain strata. Nutrient was expressed as a six-class factor from 1 for very low to 5 for very high and 6 for unknown. Differences in response to this factor by different eucalypt species have been shown to accord with general knowledge of species' nutrient responses (Ryan *et al.*, 1995; Austin *et al.*, 1997).

### 5. Biota, disturbance and time

Lack of information and suitable predictors precluded the use of these variables. The forests in the study area have been heavily logged, and there are frequent fires, but it is not thought that this has led to local extinction of *E. fastigata*. The forests are assumed to be in quasi-equilibrium with the current environment in the absence of evidence to the contrary.

### 6. Indirect surrogate predictors

In the absence of suitable direct variables for use as predictors of local environmental and soil conditions, distal indirect predictors need to be used. Differences in lithology result in differences in soil properties such as texture, fertility and depth. The topographic sequence from ridge to gully will determine a soil catena with a similar variation in properties. These environmental properties will influence soil fertility and moisture availability indirectly. Lithology was represented as a six-level factor, with classes of volcanics, hard sediments, soft sediments, granites, others, and Quaternary alluvial sediments. Topographic position was represented as a six-level factor, with classes of ridge, slope, lower slope, gully, flat, and other, derived from field observation and GIS (CSIRO Division of Wildlife and Ecology, 1996).

## Statistical model

We used generalized additive modelling (GAM) as implemented in S-PLUS® 8 for Windows, Academic Site-Edition

(Tibco Software, Palo Alto, CA, USA), testing four degrees of freedom for each variable, with stepwise backwards elimination to remove variables. Change in deviance was assessed using the significance test criterion ( $P < 0.01$ ) for dropping predictors to reach the final model. We fitted the GAMs for climate variables only (MAT, MSR, MAR), and the seven-predictor model of climate-plus-landscape variables (WinRad, NUTR, TOPO, LITH). We treated June mean daily radiation (WinRad) as a landscape predictor, as the major variation in this variable resulted from local slope and aspect. The difference between the climate-only and the climate-plus-landscape models was tested using change in deviance, following the results of Murtaugh (2009). The ecological rationality of the resulting models was examined in terms of response shapes, surfaces in environmental space and the species predicted geographical distribution.

We limited the statistical modelling to a single procedure and a single simple measure of fit, without splitting the data set into a training set and a validation set. Our aim was not to maximize prediction but to demonstrate the relative influence of landscape predictors. We tested a single species only, but it may be noted that models for over 100 species produced for unpublished consultancy reports support the importance of landscape predictors in this region (e.g. CSIRO Division of Wildlife and Ecology, 1996).

### Climate change scenario

A climate change scenario generated from the CSIRO Mark 3.0 global climate model (Randall *et al.*, 2007) was used to examine the impact of climate change on predicted species distribution. The OZCLIM scenario generator developed by CSIRO Atmospheric Research and the International Global Change Institute (<http://www.csiro.au/ozclim/home.do>) was used. In OZCLIM, regional scenarios are generated by linearly regressing the local seasonal mean temperature (or rainfall) against global average temperature, in order to generate, at each grid point (approximately 25 km apart), a change (e.g. regional temperature or rainfall) per degree of global warming. The grid point values can then be mapped to obtain a pattern of response that can be scaled according to an estimate of total global warming (Whetton *et al.*, 2001). For the purposes of this study, changes in temperature and rainfall, as well as in summer rainfall, were extracted from the model and expressed as change (actual difference in temperature and percentage difference in rainfall) relative to a baseline period of 1988 to 1999. We examine one global warming trajectory based on the 'medium' (A1B) emission scenario using predictions for 2050 (Randall *et al.*, 2007). These estimates were then down-scaled to the 100-m pixel resolution using bilinear interpolation; we regard this procedure as minimizing the likely impact of differences in landscape properties. Evaluation of the differences between the two models under climate change was undertaken by comparing maps for degree of difference in distribution and pattern of difference.

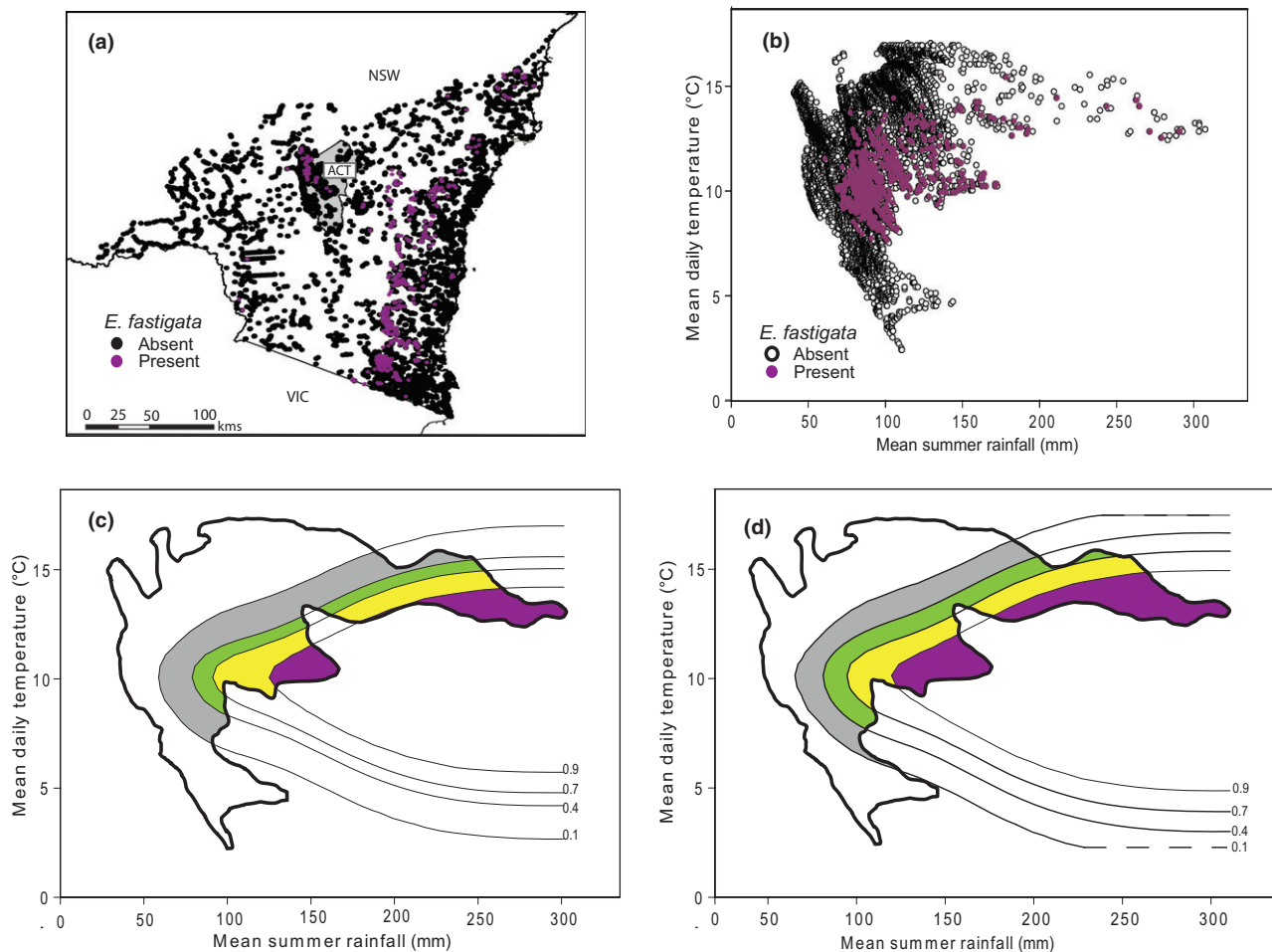
## RESULTS

The species shows a disjunct geographical distribution (Fig. 1a) and a more coherent pattern in the climate space of the two major predictors (Fig. 1b). Mean annual temperature and summer rainfall are relatively independent ( $r = 0.221$ ). The sample of 10,577 plots was overlaid on the climate space for all pixels and found to provide a detailed and unbiased representation of the climate space estimated for the study region (results not shown).

### Models of current distribution

The GAM using only the three climate predictors (MSR, MAT, MAR) is highly significant based on the chi-square test for change in deviance. The response curves are not shown, as they are almost identical to those of the full model that included the terrain predictors. The climate-plus-landscape model with seven predictors (MSR, MAT, MAT, WinRad, NUTR, TOPO, LITH) after backwards elimination tests gave a model with six predictors. The factor 'nutrients' was non-significant at the 5% probability level. The response curves and partials for the factors are provided in Appendix S1 in the Supporting Information. *Eucalyptus fastigata* has unimodal responses to temperature (MAT) and June radiation (WinRad), and a hyperbolic response to summer rainfall (MSR). The response to topography indicates a preference for gullies, while the preferred lithology is granites. All responses are ecologically reasonable (see Appendix S1 for details) and are consistent with general knowledge of the species' distribution and ecology (Costin, 1954; Ingwersen, 1983). The model is also consistent with previous published models for *E. fastigata* based on a subset of the current data (Austin, 1992, 1998; Austin *et al.*, 1994). Response surfaces are shown for the climate space for the climate-only model (Fig. 1c) and for optimal conditions for the other predictors (Fig. 1d). There has been no thresholding of probability contours to create presence/absence maps because the contours are more informative when comparing models of the same species. We adopt as a convention that the qualitative environmental realized niche (QERN, Austin *et al.*, 1990) has a predicted probability of occurrence greater than 0.1, and the optimal niche is represented by predictions above 0.7. Large areas of the climate space are predicted to provide optimal conditions *but most of these are outside the limits of the climate data space on which the models were based* (Fig. 1c, d). Correlative models are expected to be robust within the predictor space of the training data, but areas that are extrapolated beyond this data space have the potential to be unstable and poorly predicted. This type of extrapolation is considered risky and contrary to the intention of such models. Whether the extrapolation into these regions has any validity depends on the proximal nature of the predictor variables, and if there are any missing or unknown variables whose influence may become operative in that part of the climate space. The optimal QERN is from 10° to 14 °C, with an increasing requirement for summer rainfall above





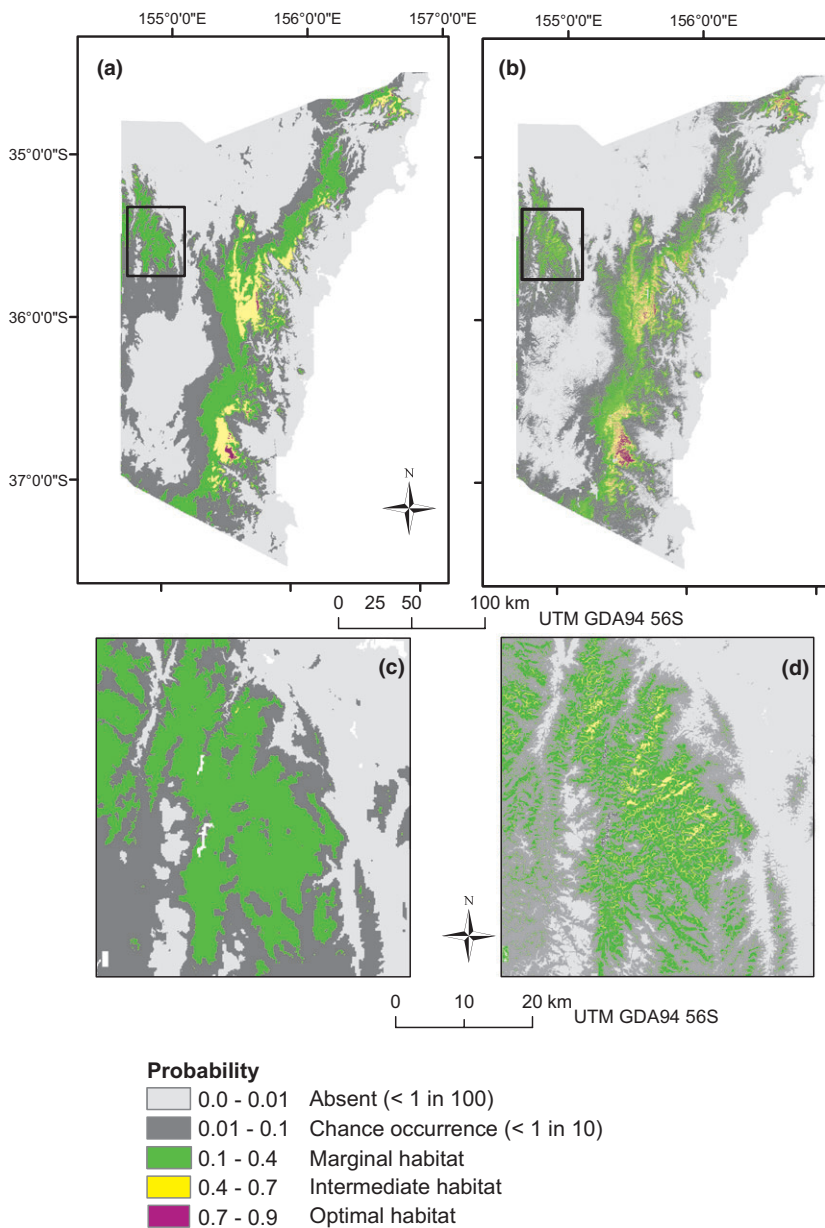
**Figure 1** (a) Observed distribution of *Eucalyptus fastigata* in the study area in south-eastern New South Wales, Australia, based on 10,577 presence/absence plots; (b) distribution of *E. fastigata* in the equivalent climatic space of mean annual temperature and mean summer rainfall for the same area; (c) predicted probability of occurrence of *E. fastigata* for the climate-only model with mean annual rainfall set to 800 mm; and (d) predicted probability of occurrence of *E. fastigata* for a climate-plus-landscape model with landscape predictors set for maximum occurrence (i.e. mean June daily radiation = 6 MJ m<sup>-2</sup> day<sup>-1</sup>; lithology = granites; topographic position = gully). Outlines in (c) and (d) represent the climate envelope for the study area.

150 mm with increasing temperature (Fig. 1c, d; Appendix S1). There is no evidence to support the existence of an optimal QERN below 10 °C, as those conditions are outside the data space of the GAM and do not exist in the study area. The curvilinear influence of annual rainfall (see Appendix 1) has a small but noticeable effect on the predicted probabilities, changing the maximal areas of optimal niche to 800 mm MAR, with declines at 500 mm and 1100 mm. The climate-plus-landscape model shows similar patterns. There are progressive expansions of the optimal area into lower-rainfall areas on protected southern gully sites (Fig. 1d), and contractions on exposed northern slopes (not shown).

The pattern of probability classes in environmental space does not necessarily indicate the spatial extent of these classes in the predicted geographical distribution of the species. The current distribution as predicted by the climate-only model (Fig. 2a) shows extensive areas predicted to represent the QERN of the species (probability of occurrence above 0.1) and

several large patches along the coastal scarp where the probability is above 0.4, but very few areas where the optimal niche (probability > 0.7) is to be found. The pattern of distribution predicted by the climate-plus-landscape model (Fig. 2b) for the study area appears similar to that for the climate-only model. However, the map shows a more fragmentary pattern of occurrences of different levels of probability. There are now numerous small local areas with optimal niche conditions, which occur on protected south-facing lower slopes and gullies.

For the climate-only model there are no regions in the western enlargement of the Brindabella Range area where *E. fastigata* is predicted to occur with a probability greater than 0.4 (Fig. 2c). For the climate-plus-landscape model, the Brindabella Range now shows areas with intermediate niche conditions (Fig. 2d), which accords well with local knowledge (Costin, 1954; Ingwersen, 1983). In summary, the climate-only model predicts 5870 ha of optimal habitat ( $P > 0.7$ ), as



**Figure 2** Predicted distribution of *Eucalyptus fastigata* in south-eastern New South Wales, Australia, under current climate conditions using GIS with 100-m resolution. (a) Predicted distribution using a climate-only model; (b) predicted distribution using a climate-plus-landscape model; (c) enlarged map predictions for Brindabella Range area using a climate-only model; and (d) enlarged map predictions for Brindabella Range area using a climate-plus-landscape model.

compared with 21,895 ha for the climate-plus-landscape model, constituting a nearly fourfold increase in optimal habitat. The climate-only model fails to predict how extensive optimal niche conditions for the species are. The inclusion of local landscape properties as predictors shows that local refugia may exist in areas otherwise regarded as sub-optimal when using only climate variables.

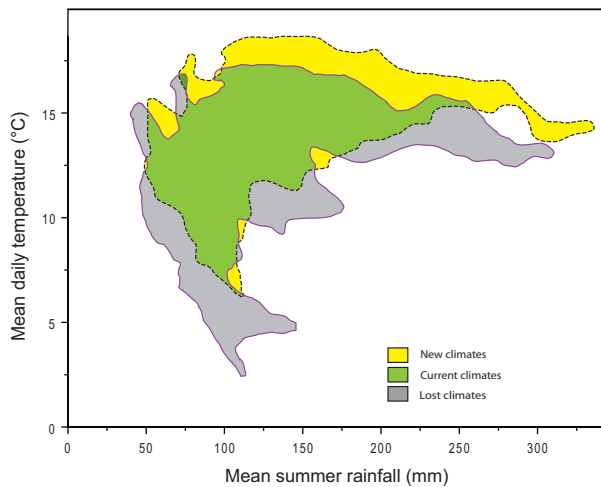
### Predicted future distribution under climate change

The predicted change from the present conditions in the climate space for 2050 is shown in Fig. 3. The most extreme outcome in this scenario is the disappearance of the low-temperature alpine climates, which will no longer occur in the region. The selected scenario predicts new conditions to be only slightly warmer (averaging 2.6 °C) than the current

climate. From the position of the response surfaces (Fig. 1c, d), the limited extrapolation to higher temperatures using the existing models is likely to be robust, that is, unlikely to cross any major threshold responses in the 0.5 °C temperature change across the study site (Fig. 3).

There are major differences predicted by the climate-only model (Fig. 4a). Areas in the north-east of the study area become marginal for the species, as do areas on the coastal scarp in the central latitudes. Elsewhere, niche conditions are predicted to improve but to remain below optimal conditions. The higher elevations present in the Brindabella Range provide for the predicted expansion of distribution and increase in suitability of the environment for *E. fastigata* with the climate-only model (Fig. 4c).

Similar patterns are seen with the climate-plus-landscape model predictions (Fig. 4b). Some niche conditions are



**Figure 3** The outline shows the predicted distribution of all plots sampled in climate space under current climate conditions with the climate change scenario overlaid on the outline. For the study location (south-eastern New South Wales), see Fig. 2. 'New climates' refers to new or novel climates for this area under a climate change scenario generated from the CSIRO Mark 3.0 global climate model. We examine one global warming trajectory based on the 'medium' (A1B) emissions scenario using predictions for 2050 (Randall *et al.*, 2007).

predicted to remain  $>0.4$  along the coastal scarp (Fig. 4b), and opportunities for expansion will exist inland. For the climate change scenario, the predicted optimal habitat ( $P > 0.7$ ) for the climate-plus-landscape model (15,167 ha) is still almost twice as large as that for the climate-only model (8299 ha). The climate-plus-landscape model predicts that the Brindabella Range will have extensive areas of species optimal conditions, becoming a core area for the species (Fig. 4d). Local refugia will still exist on the coastal scarp (Fig. 4b), and opportunities for expansion will exist inland. Landscape properties in this region buffer the existence of this species against the climate change scenario used.

## DISCUSSION

Making a conceptual model of species/environment interactions explicit, for example in equation 1, allows more informed discussion and analysis of current SDM research, although we recognize that equation 1 is little more than a checklist of variables to be included. By evaluating the relative importance of climate and landscape variables such as radiation, it has been shown that different outcomes may occur under climate change from modelled distributions developed using climate-only variables. If a predictor known to be potentially important based on ecological knowledge is omitted, then the model will be inadequately specified and the results potentially biased. This is always possible with correlative models; problems arise when the omission is not recognized and tested.

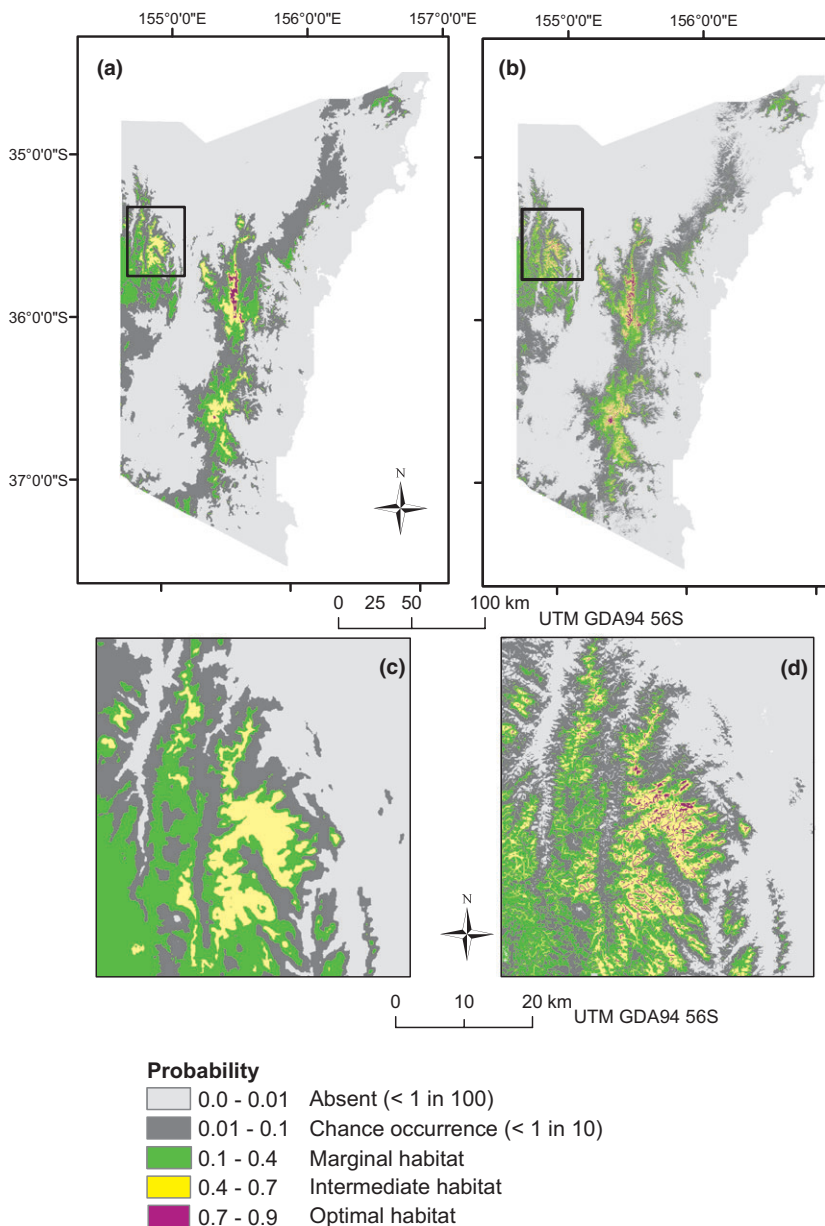
Earlier researchers using climate-only predictors based on an ecophysiological conceptual model (Prentice *et al.*, 1992;

Huntley *et al.*, 1995; Sykes *et al.*, 1996) were careful to outline some of their assumptions. Huntley *et al.* (1995) used locally weighted regression to model the responses of eight selected European species to climate and two possible future changes in climate. The species data were derived from atlas data at a  $50 \times 50$  km scale. Three bioclimatic variables were included in the models as predictors: mean temperature of the coldest month (MTCO), growing degree-days, the temperature sum above a  $5^\circ\text{C}$  threshold (GDD5), and the ratio of actual to potential evapotranspiration (AET/PET). This ratio was calculated based on climatic variables plus a GIS layer for soil water capacity, a proximal predictor derived from a water-balance model based on known ecophysiological processes and using a distal indirect variable such as soil water capacity. Huntley *et al.* (1995) carefully discussed the discrepancies between the observed and predicted distribution maps for each species, recognizing the potential influence of calcareous substrates and pH on distributions. In considering the possible reasons for discrepancies they mention '(1) the species' range is not in equilibrium with the present climate; (2) the climate of the mean elevation of those 50 km squares where the species occurs is not representative of the climate where the species grows; and (3) the species' range is determined by some other aspect of the climate apart from the three variables used in the present study' (p. 987). These three issues, plus the potential for non-climatic variables to limit distribution, are still with us today.

The assumption that coarse-scale data (e.g.  $50 \times 50$  km grid cells) are sufficient to create robust predictions requires testing. For such data to be used it must be shown that the models obtained are sufficiently adequate for the intended purpose as compared with using data of higher resolution. A comparison of climate-only and climate-plus-landscape predictions (Figs 2 & 4) at high resolution shows major changes in the potential quality of habitat over short distances when landscape is included, which will buffer against regional extinction. Low-resolution climate-only models simply cannot capture these phenomena.

Luoto & Heikkinen (2008) investigated whether the inclusion of topographical heterogeneity in SDMs for butterflies altered conclusions regarding their changed distributions under climate change scenarios. Their measure of topographical heterogeneity was the difference in elevation between the highest and lowest points based on a 1-km GIS when using  $30' \times 60'$  grid cells. In mountainous areas, climate-topography models predicted only half the species losses that a climate-only model predicted. In flat regions, climate-topography models predicted twice the losses of the climate-only models. The authors concluded that failure to incorporate topographical heterogeneity into broad-scale SDMs introduced a significant source of error. Topography (expressed as range in elevation) was the only non-climatic variable examined. This study identifies heterogeneity within grid cells as giving rise to inadequacies in predicting response to climate change. Other environmental variables might have similar effects.

Topographic position as an indirect factor reflects the soil catena with increasing soil depth, available soil moisture and



**Figure 4** Predicted distribution of *Eucalyptus fastigata* in south-eastern New South Wales, Australia, under climate change scenario conditions. (a) Predicted distribution using a climate-only model; (b) predicted distribution using a climate-plus-landscape model; (c) enlarged map predictions for Brindabella Range area using a climate-only model; and (d) enlarged map predictions for Brindabella Range area using a climate-plus-landscape model.

nutrients. Lithology captures differences in fertility and other soil properties. The combination of June radiation and these factors defines for *E. fastigata* a highly local optimal niche, which will be buffered against changes and can only be identified with high-resolution GIS layers. Survival in areas where climate change is detrimental to species growth will depend on these local habitats. Equally, in areas where climate conditions improve for a species, expansion will be conditional on other variables being suitable. Figure 4 demonstrates that the existence of local refugia owing to the moderating influence of landscape depends on specifying both local predictors and an appropriate resolution for the data. It is now becoming possible to model and predict radiation and temperatures at very high resolutions, taking local landscape effects into account (see Bennie *et al.*, 2008; Fridley, 2009), and major improvements in the biophysical predictors can be expected.

Certain other conclusions can be drawn from the results presented here that have relevance to the current practice of species distribution modelling. Figure 3 shows the congruence between the current climate space and that predicted by the particular scenario. The overlap is a measure of the confidence that can be placed in the predictions, all other things being equal. Analyses of data space overlap are important but rarely checked (see Williams *et al.*, 2007 and Platts *et al.*, 2008 for examples of overlap comparisons). Depending on the climate change assumed, a given geographical area may no longer overlap with the climate space on which the SDM was constructed, invalidating extrapolation of the statistical model. If there is overlap but not complete overlap then the robustness of the predictions will depend on the position of the species niche in the climate space. In the case of *E. fastigata*, confidence could be placed in predictions under low summer



rainfall conditions because the species' lower limits appear to have been reached within the sampled climate space. In contrast, little confidence could be placed in predictions for conditions of low temperature and high summer rainfall (Figs 1 & 3). The transferability and validity of extrapolation for an SDM critically depends on the overlap of the climate space on which the model was based and on the climate space to which it is applied. To assess the value of the SDM for predicting climate change responses we recommend showing the climate space overlap in all studies.

Considerable progress has been made in the statistical procedures for species distribution modelling (Elith & Leathwick, 2009). There has also been a significant increase in the complexity of the analyses being undertaken, with numerous statistical methods for species distribution modelling being used, with up to 10 or more climate change scenarios (Thuiller *et al.*, 2006; Guisan *et al.*, 2007; Rieckbusch *et al.*, 2008; Randin *et al.*, 2009). However, there is a need to ensure that the ecological, data and statistical models are compatible (Austin, 2002). This study has deliberately adopted a basic statistical model. There is one method, GAM, one test change in deviance, and one simple climate change scenario. Logically, climate-only models will fail to make adequate predictions if soil pH is a major determinant of distribution (Huntley *et al.*, 1995), as for example with many calcicoles in southern Britain (see also Coudon *et al.*, 2006). The simple case study models used here have been sufficient to demonstrate that current climate-only models can fail to capture an important local climatic determinant of species occurrence, when local topographic features interact to modify the regional climate variables. Further elaboration of the statistical methods or variation in scenarios is unlikely to change this result. The conceptual model defined a need for a biophysical model for estimating solar radiation, exposing the importance of aspect and the possible importance of topographic variation in soils. This, in turn, defined the resolution size for observations as part of the data model required for the SDM.

For trees, there is a scale that captures the main environmental influences affecting their growth and survival. This will be at a plot resolution where environmental variables are homogenous relative to the size of the trees. As plots increase in size and hence in environmental heterogeneity, so the signal relating trees and the environment will degrade. There is a natural resolution size that captures the principal environmental variables influencing trees. This scale of resolution varies with the organism, whether trees, forbs or territorial birds. The spatial resolution of an SDM should be determined by the biology of the organism and not by the availability of data.

Statistical elaboration is no substitute for incremental testing of assumptions.

## CONCLUSIONS

We conclude that current best practice for the use of SDMs needs to be revised with respect to its ecological framework, particularly in relation to climate change scenarios.

1. An explicit case should be made for the inclusion and exclusion of environmental processes, particularly non-climatic processes.
2. The resolution of the data should be commensurate with the ecological processes being postulated as important to the growth and survival of the species.
3. A special case is necessary to justify the application of an SDM to climate space beyond the boundaries of the space on which the model was based.
4. Recognition is needed that local landscape properties are critical predictors in determining current and potential distributions of species.

The case study demonstrates that the lack of landscape predictors in an SDM may lead to interpretations of the impact of climate change that are unduly pessimistic. Species may need only to disperse across a valley to reach a suitable habitat, rather than to migrate hundreds of kilometres in latitude or hundreds of metres up an elevational gradient, if available. Local landscape properties modify regional climatic conditions, often creating optimal environments for species. These same local landscapes will provide, under climate change scenarios, refugia and opportunities for local expansion as well as reductions in distribution. Where natural vegetation cover is continuous, estimates of species extinctions under climate change are overly pessimistic, as in this study area. Where clearing of vegetation is extensive, then pessimistic estimates may well be justified.

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## SUPPORTING INFORMATION

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

**Appendix S1** Response curves with standard errors for the fitted probabilities of occurrence as calculated by modelling the original sample data with the climate plus landscape model for *Eucalyptus fastigata*.

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