Primary research article

Which species distribution models are more (or less) likely to project broad-scale, climate-induced shifts in species ranges?

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A B S T R A C T

Species distribution models (SDMs) frequently project substantial declines in the spatial extent of climatically suitable habitat in response to scenarios of future climate change. Such projections are highly disconcerting. Yet, considerable variation can occur in the direction and magnitude of range changes projected by different SDM methods, even when predictive performance is similar. In this study, we assessed whether particular methods have a tendency to predict substantial loss or gain of suitable habitat. In particular, we asked, "are 14 SDM methods equally likely to predict extreme changes to the future extent of suitable habitat for 220 Australian mammal species?". We defined five non-mutually exclusive categories of 'extreme' change, based on stability or loss of current habitat, or the dislocation of current and future habitat: a) no future habitat (range extinction); b) low stability of current habitat ($\leq$10% remains); c) no gain of habitat in new locations; d) all future habitat is in new locations (i.e. completely displaced from current habitat); and e) substantial increase in size of habitat (future habitat is $\geq$100% larger than current). We found that some SDM methods were significantly more likely than others to predict extreme changes. In particular, distance-based models were significantly less likely than other methods to predict substantial increases in habitat size; Random Forest models and Surface Range Envelopes were significantly more likely to predict a complete loss of current habitat, and future range extinction. Generalised Additive Models and Generalised Linear Models rarely predicted range extinction; future habitat completely disjunct from current habitat was predicted more frequently than expected by Classification Tree Analysis and less frequently by Maxent. Random Forest generally predicted extreme range changes more frequently than other SDM methods. Our results identify trends among different methods with respect to tendency to predict extreme range changes. These are of significance for climate-impact assessments, with implications for transferability of models to novel environments. Our findings emphasise the need to explore and justify the use of different models and their parameterisations, and to develop approaches to assist with optimisation of models.

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1. Introduction

Contemporary anthropogenic climate change has already resulted in shifts in the range margins of numerous, diverse taxa (Melles et al., 2010; Chen et al., 2011; Garroway et al., 2011; Rubidge et al., 2011), and paleoecological data suggest that range shifts were the norm during previous episodes of climate change (Birks, 1989; Huntley, 1990; Graham, 1992; Willis and MacDonald, 2011).

Understanding the extent to which species' distributions may shift in response to climate change over the course of this century and beyond may assist in identifying species vulnerable to climate change, prioritising conservation efforts, and developing optimal adaptation and land management plans.

Correlative species distribution models (SDMs) are frequently used to examine the potential for changes to the distribution and quality of habitat under scenarios of future climate (Franklin, 2010). This approach is based on the assumption that the location of populations reflects the environmental preferences and tolerances of a species (Guisan and Thuiller, 2005). Models of this relationship, based on the observed subset of those populations, can then be used

to assess the suitability of a region, for a particular species, under current, past or future climate. Such climate change experiments assume that relationships inferred from historical data remain consistent under a changing climate (Maraun, 2012).

Predictions of broad-scale changes in species' distributions in response to climate change have contributed to substantial concern regarding the fate of biodiversity in a warming world (e.g. Thomas et al., 2004; Ben Ras Lasram et al., 2010; Sauer et al., 2011; Ihlow et al., 2012; Ochoa-Ochoa et al., 2012; Warren et al., 2013). Numerous studies indicate that, under climate change, a sizeable proportion of species will be faced with an absence of suitable habitat (range extinction), or future habitat that is completely disjunct from current habitat. For example, ∼24% of Mexican amphibian species are at risk of losing all habitat by 2080 (Ochoa-Ochoa et al., 2012), while habitat for nearly 12% of the world's Chelonian species may lie in areas currently unsuitable (Ihlow et al., 2012). Depending upon the scenario of greenhouse gas emissions, 11–19% of 1541 seed plants in Alberta, Canada, were predicted to lose > 90% of current habitat by 2080 (Zhang et al., 2015). Similarly, an analysis of 2954 species across North and South America predicted the loss of all existing habitat for at least 10% of species by 2071–2100 (Lawler et al., 2009). In one of the largest studies to date, Warren et al. (2013) estimated that after accounting for dispersal, 2–6% of 5382 animal species would lose ≥ 90% of current habitat. Hence, predictions by SDMs indicate that the rate of extinction in the 21st century may exceed estimates of historical extinction events from the fossil record. However, there is on-going debate as to the accuracy of SDMs and whether they will over- or under-estimate range changes and extinction (see review by Bellard et al., 2012).

In recent years the number of methods for fitting SDMs has increased considerably (Elith and Graham, 2009; Elith and Leathwick, 2009; Franklin, 2010), and now includes distance-based or profile models (e.g. BIOCLIM, Nix, 1986; Booth et al., 2014), statistical models that can fit complex non-linear relationships (such as Generalised Additive Models) and machine-learning techniques (Elith et al., 2008; Elith and Leathwick, 2009). These methods differ in complexity, data requirements and ease of use, and their characteristics have been well-described elsewhere (e.g. Syphard and Franklin, 2009; Franklin, 2010; Xinhai and Wang, 2013).

SDM method choice is influenced by access to software, data availability (e.g. presence only or presence/absence records), user ability and the particular goals of the study (Segurado and Araújo, 2004; Elith and Leathwick, 2009; Ahmed et al., 2015), although different disciplines and geographic regions have traditionally utilised different techniques (Elith and Leathwick, 2009). However, identification of the most appropriate SDM method is complicated by a number of factors, and multi-model comparisons have repeatedly concluded that there is no single 'best' method (Elith et al., 2006; Diniz-Filho et al., 2010).

Several studies have suggested that SDM methods with high flexibility in modelling complex species-environment relationships may outperform simpler methods (Elith et al., 2006; Tsoar et al., 2007; Li and Wang, 2013). For instance, machine-learning algorithms (such as Random Forests, Maxent and Boosted Regression Trees) frequently outperform regression-based approaches (e.g. Multivariate Adaptive Regression Splines and Generalised Linear Models) (Bucklin et al., 2015; but see Guillera-Arroita et al., 2015). Others caution the use of complex methods: while these may predict observed occurrence patterns well, they may result in overfitting, and hence may not necessarily predict an acceptable representation of the species' potential distribution (Diniz-Filho et al., 2010; Li and Wang, 2013). Models with high predictive accuracy for the data used in their calibration may also demonstrate poor transferability (or generality); that is, their performance may decline when projected onto different geographic regions (Heikkinen et al., 2012) or time periods (Fronzek et al., 2011). The Random Forest model, for example, generally has high predictive capacity as determined by AUC (the area under the receiver-operating characteristic curve) calculated on data similar to those used for model-fitting (Coetzee et al., 2009; Virrkala et al., 2010; Yen et al., 2011). However, this model has been shown to have lower transferability than other SDM methods, such as Generalised Linear Models (Heikkinen et al., 2012; Crimmins et al., 2013).

Different SDM methods may also have similar predictive performance (e.g. as quantified by the AUC or True Skill Statistic [TSS]; Allouche et al., 2006) yet generate very different predictions of suitable habitat (Beaumont et al., 2009; Parviainen et al., 2009; Syphard and Franklin, 2009). These differences can be magnified when models are projected onto alternative climate scenarios (for which there is also no 'best' choice), with different SDMs varying in the magnitude and direction of predicted changes (Pearson et al., 2006; Beaumont et al., 2007, 2008). Model performance can also be influenced by a species' characteristics and its distribution data (Syphard and Franklin, 2009; Dobrowski et al., 2011; García-Callejas and Araújo, 2015), selection of predictor variables (Barbet-Massin and Jetz, 2014) and geographic location (Engler et al., 2011). As such, the choice of SDM method constitutes the primary source of variation in predictions of species' future distributions (Buisson et al., 2010; Garcia et al., 2012).

These factors have led to the current trend to combine multiple models into 'ensembles' (Araújo and New, 2007; Beaumont et al., 2009; Marmion et al., 2009; Grenouillet et al., 2011; Garcia et al., 2012; Xinhai and Wang, 2013). Ensemble modelling experiments can then be used to distinguish regions of model consensus (i.e. where most models agree that the environment is suitable/unsuitable) from regions where there is disagreement. A number of studies have found that ensembles outperform individual models (Marmion et al., 2009; Yen et al., 2011; Grenouillet et al., 2011; Crossman et al., 2012), however, the use of ensembles can still be problematic (Elith et al., 2010; Rapacciuolo et al., 2012; Crimmins et al., 2013) as errors/biases in individual SDMs may lead to incorrect conclusions being drawn from the ensemble.

While previous studies have assessed sources of variation in SDM output (e.g., Dormann et al., 2008; Nenzén and Araújo, 2011; Watling et al., 2015), less attention has been given to whether particular SDM methods are biased towards predicting substantial loss or gain of suitable habitat, and if so, why. Therefore, in this study, we explored 'extreme' range changes predicted by 14 SDM methods incorporated into the R packages *biomod2* (Thuiller et al., 2012) and *dismo* (Hijmans et al., 2011). In particular, we asked whether these SDM methods predicted 'extreme' range changes with equal frequency. We defined five non-mutually exclusive categories of extreme change, based on stability or loss of current habitat or the dislocation of current and future habitat: a) no future habitat (range extinction); b) low stability of current habitat (i.e. ≤ 10% of current habitat remains, although future habitat may be predicted in new locations); c) no gain of habitat in new locations (future habitat is identical to, or a subset of, current habitat); d) all future habitat is in new locations (future habitat does not overlap with current habitat); and e) substantial increase in size of habitat (i.e. future habitat is at least twice the size of current habitat). We modelled future habitat suitability for 220 mammal species across Australia and compared the proportion of predictions from each SDM method that calculated these extreme range changes.

2. Methods

2.1. Species records

For this study, we focused on native terrestrial mammal species in Australia, as their distributions are generally well known and