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**Title:** Unpacking the mechanisms captured by a correlative SDM to improve predictions of climate refugia

**Running head:** Robust predictions of climate refugia

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## Abstract

Climate refugia are regions that animals can retreat to, persist in, and potentially then expand from under changing environmental conditions. Most forecasts of climate change refugia for species are based on correlative species distribution models (SDMs) using long-term climate averages, projected to future climate scenarios. Limitations of such methods include the need to extrapolate into novel environments and uncertainty regarding the extent to which proximate variables included in the model capture processes driving distribution limits (and thus can be assumed to provide reliable predictions under new conditions). These limitations are well documented, however, their impact on the quality of climate refugia predictions is difficult to quantify. Here we develop a detailed bio-energetics model for the koala. It indicates that range limits are driven by heat-induced water stress, with the timing of rainfall and heat waves limiting the koala in the warmer parts of its range. We compare refugia predictions from the bio-energetics model with predictions from a suite of competing correlative SDMs under a range of future climate scenarios. SDMs were fitted using combinations of long-term climate and weather extremes variables, to test how well each set of predictions captures the knowledge embedded in the bio-energetics model. Correlative models produced broadly similar predictions to the bio-energetics model across much of the species' current range – with SDMs that included weather extremes showing highest congruence. However, predictions in some regions diverged significantly when projecting to future climates due to the breakdown in correlation between climate variables. We provide unique insight into the mechanisms driving koala distribution and illustrate the importance of subtle relationships between the timing of weather events, particularly rain relative to hot-spells, in driving species-climate relationships and distributions. By unpacking the mechanisms captured by correlative SDMs, we can increase our certainty in forecasts of climate change impacts on species.

## Introduction

Considerable emphasis has been placed on identifying climatic refugia – regions that animals can retreat to, persist in, and potentially then expand from under changing environmental conditions (Keppel *et al.*, 2012). Refugia can include locations currently occupied by the species that remain suitable (*in situ* refugia), as well as currently unoccupied locations that can support the species as conditions change (*ex situ* refugia) (Ashcroft, 2010). Most commonly, refugia are identified using correlative species distribution models (SDMs), whereby the current distribution of a species is used to develop a model which statistically associates distribution with environmental layers (Peterson *et al.*, 2002, Thomas *et al.*, 2004). Refugia are then identified by projecting which areas will fall within the species 'environmental envelope' under future climates (Guisan *et al.*, 2005). These models can be built with little or no information about the species (aside from distribution records) and have the potential to implicitly capture both abiotic and biotic processes that limit species distributions (Elith & Leathwick 2009). However, this approach has a number of limitations when used to identify refugia under future anthropogenic climate change, including complications arising from deriving habitat suitability models from biased occurrence data (Guillera-Arroita *et al.*, 2015), the need to extrapolate when projecting models to no-analogue conditions (Fitzpatrick & Hargrove, 2009), and failure to explicitly capture biotic interactions and demographic processes that may strongly influence population persistence within refugia (Thuiller *et al.*, 2013). Here we focus primarily on the assumption that the relationship between proximate variables included in the models and the processes they implicitly capture remains constant (Guisan *et al.*, 2005, Elith & Leathwick, 2009, Jackson *et al.*, 2009).

Animals inhabit fluctuating environments, experiencing weather rather than the long-term climate averages typically used to model their distributions. Daily, seasonal and inter-annual variations in environmental conditions can influence species' distribution and abundance (Parmesan *et al.*, 2000, Reside *et al.*, 2010, Wernberg *et al.*, 2013) and an approach that captures these is needed to provide more robust predictions of refugia under future changes in climate. Recent extreme weather events have been linked to high mortality and reduced reproductive success in a range of taxa including birds, bats and arboreal mammals (Welbergen *et al.*, 2008, Catry *et al.*, 2011, Lunney *et al.*, 2012). Increased frequency or severity of these events in the future (Easterling *et al.*, 2000, Jentsch *et al.*, 2007) could lead to local extinction of species within these areas (Wernberg *et al.*, 2013), even if the average conditions remain suitable. Not surprisingly, a number of studies have found that species distribution models that include variables that quantify inter-annual variation in climate (Zimmermann *et al.*, 2009) or weather data that captures extremes such as drought and heat waves (Reside *et al.*, 2010, Bateman *et al.*, 2012) were better able to accurately identify suitable habitat under the current climate.

As well as better capturing how species are distributed currently, models that explicitly include effect of weather on species are important because the relationship between mean climate and extreme weather events is likely to change in the future. In some regions of the world, temperature extremes during particular seasons are projected to scale with changes in global annual mean temperature by a factor of more than two (Orlowsky & Seneviratne, 2012). Physiologically stressful environments also frequently arise from interactions between multiple environmental conditions. For example, thermal stress for mussels in the intertidal zone is dependent on whether low tide (mussel exposure) coincides with the warmest part of the day (Helmuth *et al.*, 2002). For mammals or birds that rely on evaporative cooling for temperature regulation, hot weather is most stressful during dry periods where access to water is limited (Albright *et al.*, 2010, Krockenberger *et al.*, 2012). In such cases, it is particularly important to model these interactions explicitly because any changes in the relationship between these variables in the future could lead to misleading conclusions about climatically suitable habitat if a single correlated variable is used as a proxy.

Biophysical ecology is a powerful approach with which to investigate how climate influences survival and reproductive output of individuals, and to make inferences about current and future species distributions (Porter & Gates, 1969, Buckley, 2008, Kearney & Porter, 2009). Biophysical models are based on the physical principles of energy and mass transfer (Bird *et al.*, 2002) and describe the exchange of energy, nutrients and water between organisms and their physical environment. They can be used to predict the energy and water requirements of endotherms based on their physiology, morphology and behaviour, as well as the microclimates they experience (Porter *et al.*, 2000, Porter & Mitchell, 2006). Using this approach it is possible to predict where species could survive and reproduce under both current and future climate by coupling predicted energy and water requirements with information on the amount of energy and water available to individuals (Kearney *et al.*, 2013).

In this modelling framework, an animal's response to its environment can be simulated on an hourly basis using daily weather data, making it possible to capture a range of processes, including extremes, which limit species distributions. The combined effects of factors such as temperature, humidity and water availability on heat exchange, water balance and survival are explicitly modelled, meaning that predictions of animal responses under future climate scenarios are robust to changes in the relationships between these variables. As well as enabling predictions of species distribution shifts under climate change, this mechanistic approach grants insight into why these shifts are likely to occur, allowing us to identify and explore prediction uncertainty. For example, one can quantify the effect of differences in projected changes in key climate drivers, assess the potential for adaptation in key traits (Kearney *et al.*, 2009), or assess the likely impacts of concurrent changes in habitat properties (Kearney, 2013).

Despite the utility of process-based approaches such as bio-energetics modelling, evaluation of climate change impacts on species' are most frequently based on SDM predictions (Guisan *et al.*, 2013). A number of studies have examined how modelling approach, assumptions about of future climates (emissions scenario and general circulation model), and the number and type of predictor variables, can influence correlative model predictions (Elith & Graham, 2009, Buisson *et al.*, 2010, Synes & Osborne, 2011). An important but often neglected source of uncertainty is that, when used to project climate change impacts, correlative approaches assume that the relationship between proximate variables included in the models and the processes they implicitly capture remains constant (Guisan *et al.*, 2005, Elith & Leathwick, 2009). This is difficult to assess because we seldom know which processes are limiting a species distribution the most, and there is considerable uncertainty about how environmental factors will change in the future.

Here, we develop a fine spatial and temporal scale endotherm energetics model which describes the fundamental niche of the koala from a thermodynamic point of view, and use it to evaluate correlative models of the same species using daily and annual weather data under a variety of climate change scenarios. We consider the mechanisms driving the koala distribution at local to continental scales and investigate where and why process-based and correlative model predictions of refugia differ. Insight gained by 'unpacking' the mechanisms captured by different modelling approaches can help improve predictions of climate refugia and identify key sources of uncertainty in future projections.

## Materials and methods

### *Study species*

The koala, *Phascolarctos cinereus*, is broadly distributed across eastern Australia (Fig. 1 - insert). Koalas feed predominantly on Eucalyptus foliage, a poor quality food source (Moore & Foley, 2000), and food intake is likely to be constrained by a relatively small body size. Foliage is also the primary source of water for koalas, particularly during dry periods when free water is not available in the environment. Koalas do not typically use any form of den but reduce heat loads by seeking shade and cool tree trunks during hot weather (Briscoe et al., 2014, Crowther et al., 2014). High koala mortality has been observed during extreme heat events that coincide with periods of low rainfall (Gordon *et al.*, 1988).

### *Biophysical model*

To generate bio-energetic predictions of climate refugia for koalas we used Niche Mapper (Porter *et al.*, 2000, Porter & Mitchell, 2006), a modelling framework that calculates energy and water requirements of animals based on their behavioural, morphological and physiological traits, and the microclimates available to them. Niche Mapper consists of a microclimate model and an animal model. The microclimate model translates location, terrain and weather station data (daily air temperature, wind speed, cloud cover and humidity) into the range of microclimatic conditions available to the animal based on properties of the environment specified by the user (e.g. slope, aspect, soil properties, available shade) (Porter *et al.*, 1973, Kearney *et al.*, 2014).

The animal model then uses the principles of heat and mass transfer to determine the metabolic rate and water turnover required for the animal to maintain the core body temperature within specified limits, based upon its traits and the range of microclimates available to it (Porter &  Mitchell, 2006, Porter *et al.*, 2006). Input data used to model koalas included the range and order of thermoregulatory behaviours (e.g. shade seeking behaviour, postural changes), as well as morphological data (body dimensions and shape, fur characteristics) and physiological data (core temperature, target metabolic rate; see Table S1). Niche Mapper first calculates heat-fluxes using the initial conditions specified by the user. If the predicted hourly metabolic rate is more than 2.5% above or below the minimum metabolic rate, a set of thermoregulatory behaviours, and then physiological adjustments, are enacted to bring the predicted metabolic rate closer to minimum levels (Table S1). Once the predicted metabolic rate is within the allowable range, or if all thermoregulatory options are exhausted, the program moves onto the next hour, with all input parameters (e.g. posture, fur properties) reset to initial values. This version of the model assumes that the animal reaches a thermal steady state within each hour. The Niche Mapper model performs well in describing koala energy and water requirements when tested against metabolic chamber and field data collected during hot, dry conditions that are of primary interest here (Briscoe, 2014).

We identified climate refugia by modelling habitat suitability for reproducing females because for populations to persist individuals must successfully reproduce. In addition, limitations on lactating females appear to restrict koala distributions in hot inland and northern areas (Briscoe, *unpublished data*), and populations within these regions are most likely to be affected by climate change. Daily water and energy requirements for lactation in females were estimated by splining measurements of milk-energy intake by offspring (assumed to equal milk production) made at seven time points during lactation (Krockenberger *et al.*, 1998), and combining these with milk composition data (Krockenberger, 1996; Table S1). Koalas vary in morphological traits (body size and fur) across their range, which alters their sensitivity to climate (Briscoe *et al.*, 2015). We modelled koalas with site-specific body size and fur properties estimated from current geographic clines in traits (Briscoe *et al.*, 2015), thus making the assumption that morphological clines remain constant over time.

To assess current and future habitat suitability we used predicted energy and water requirements of koalas at each site to calculate how much food (*Eucalyptus* leaves) a koala would need to consume each week to meet both energy and water requirements. Food intake to meet energy requirements was estimated assuming that leaves had an energy content of 20.1 kJ.g$^{-1}$ of dry matter and that koalas were able to metabolize 45% of this energy (Nagy & Martin, 1985). To calculate food intake to meet water requirements we assumed 66% of preformed water within leaves was available to koalas and foliage water content was 56% (Nagy & Martin, 1985). Where increased food intake was required to meet water requirements, it was assumed that koalas display a flexible digestive strategy and only metabolize sufficient energy to meet requirements (Ellis *et al.* 2010). We calculated yearly habitat suitability scores ($S$) as: 1- the proportion of weeks in each year that koalas needed to increase food intake above maintenance levels (Cork *et al.*, 1983) to meet thermoregulatory costs. If predicted food intake (assuming high foliage water content – 66%) exceeded the maximum food intake rate recorded for koalas (Krockenberger, 2003) for more than one week, we set $S$ to 0. We conservatively assumed koalas could obtain sufficient free water to balance their water budget (e.g. from wet leaves) if rain in the past week exceeded 1 mm, and explored the impact of different foliage water content values (47%, 66%) on predicted distributions.

In fluctuating natural environments, the persistence of species may be influenced by temporal patterns in habitat suitability; the effect of poor years may be partially offset by subsequent good years that allow high survival and reproductive success, while prolonged periods of stress may result in local extinction (Harrison, 2000). To account for this we calculated site habitat suitability ($\bar{S}$) by taking the mean of habitat suitability scores for each 20 year period simulated, with the additional constraint that sites were classed as unsuitable ($\bar{S}$= 0) if any single generation could not survive and reproduce (i.e. suitability across any 5 year period was 0).

### *Maxent models*

We generated correlative model predictions of koala distributions using Maxent (Phillips *et al.*, 2006). We focused on Maxent because it is a widely used modelling approach that is designed for presence-only data. We obtained koala presence records from the Atlas of Living Australia (ALA: http://www.ala.org.au) as well as obtaining additional records from Australian state government agencies (see Acknowledgements). These datasets spanned 1900-2013 and included data from a range of sources including incidental observations and planned surveys (total 66314 records). We excluded all records that were not accurate to 1 km or less and records from prior to 1960, and then randomly selected one observation per grid cell (0.05° resolution). Island and coastal sample points that were not covered by the climate layers were also excluded, leaving 4387 records. Rather than absence data, Maxent takes background samples that are assumed to have the same geographic and environmental extent as the region sampled for presence data. Choice of background region can influence predicted habitat suitability and should reflect knowledge of sampling as well as the intended model application (Elith *et al.*, 2011). We generated a background layer by selecting all IBRA bioregions (Interim Biogeographic Regionalisation for Australia, Department of the Environment, 2012) that contained at least one koala presence observation, as well as bioregions immediately adjacent or surrounded by these. Tasmania was excluded because Bass Strait is likely to act as a geographic barrier to dispersal, thus the absence of koala observations from this region may reflect geographic rather than environmental range-limiting processes. Background samples *(n*=10,000) were generated by randomly sampling this layer, accounting for differences in cell area across latitude (Elith *et al.*, 2011).

We used two sets of environmental variables to model koala habitat suitability using Maxent. First, following previous studies of koalas (Adams-Hosking *et al.*, 2011, Adams-Hosking *et al.*, 2012, Santika *et al.*, 2015) we modelled koalas with two variables calculated from long-term climate averages: mean annual rainfall and mean maximum summer temperature (mean temperature of the warmest period). Second, using daily weather data we generated five candidate variables that we believed reflected processes that drive koala distributions: maximum run of dry days (days with <1mm of rainfall), 95th percentile temperature (T95), maximum run of hot, dry days (days with maximum temperatures in the 90th percentile & rainfall<1mm), and average vapour pressure during hot weather (daily maximum temperature in the 90th percentile) (Gordon *et al.*, 1988, Clifton *et al.*, 2007, Lunney *et al.*, 2012). Both 'averages' and 'extreme' variables were calculated using 20-year weather datasets for current and future (2070) climates (see below). The two variables designed to capture extreme heat effects – T95 and the maximum run of hot days – were correlated ($r = 0.69$). It is common practice to discard highly correlated variables by retaining the variable with the highest contributing weight, because including correlated variables in models can influence parameter estimates and inflate variable importance (Dormann *et al.*, 2013; although see Elith *et al.*, 2011). Since our aim was to compare predictions generated using variables that captured the processes we believed limit koala distributions and we had no *a priori* reason to preference one variable over the other, we ran separate models that excluded the maximum run of hot days (extremes A) and excluded T95 (extremes B). This allowed us to analyse and compare predictions of models in which climate variables show high correlation at the present time, but are predicted to diverge (show lower correlation) in future times under alternative climate scenarios.

Koalas feed predominantly on Eucalyptus trees; therefore we included Eucalyptus forest or woodland cover in all Maxent models. Using a 100m resolution land cover layer (NVIS 4.1, http://www.environment.gov.au) we calculated the proportion of 100m x 100m cells classified as Eucalyptus woodlands or forest within each 0.05° cell.

Presence-only datasets may provide a biased view of a species distribution due to uneven sampling effort. Koalas are better surveyed than many arboreal species, but sampling bias towards roads is possible (Mair & Ruete, 2016). Therefore we also included road density as a covariate in all Maxent models. We then generated predictions for a constant level of ‘sampling effort’ (*sensu* Leathwick et al., 2006, Warton *et al.*, 2013). To test the effects of this approach to modelling bias, we also built models with only environmental and landcover data (i.e. not accounting for bias) and using a bias grid approach (Phillips *et al.* 2009, Merow *et al.* 2013 – see Fig. S1). We used hinge features (beta_hinge = 2.5) as these allow for smooth, more biologically realistic response curves that reduce over-fitting and are more appropriate for predicting into new environments (Elith *et al.*, 2010). All models were built using the ‘dismo’ package in R (Hijmans *et al.*, 2013, R Core Team, 2014).

### *Future climate data*

We simulated future climate data by adding projected monthly changes in temperature, humidity, solar radiation and wind speed for 2070 onto interpolated daily weather data for 1990-2009 obtained from the Australian Water Availability Project (Raupach *et al.*, 2009, 2012). Projected changes in climate differ between general circulation models (GCMs), sometimes considerably. For example, rainfall in some regions of Australia is predicted to increase or decrease, depending on the climate model (Smith *et al.*, 2013). Because we were primarily interested in identifying climate refugia, we present predictions based on ACCESS 1.3 (Bi *et al.*, 2013), which represents a relatively dry future scenario in northern parts of the koalas range (i.e. worst case scenario). To assess whether choice of GCM is an important source of uncertainty in identifying koala refugia in the future, we also generated Maxent predictions using five other general circulation models that perform well in capturing past climate in Australia (Watterson *et al.*, 2013), provide all variables required by the biophysical model, and represent a range of possible future rainfall scenarios across eastern Australia: ACCESS 1.0 (Bi *et al.*, 2013), HadGem2-ES (Jones *et al.*, 2011), CanESM2 (Chylek *et al.*, 2011), HadGem2-CC (Martin *et al.*, 2011), and GDFL-CM3 (Griffies *et al.*, 2011). Each Niche Mapper simulation required that energy and mass balances were solved every hour for 20 years at 114,000 sites across eastern Australia (~20 billion calculations). Due to these computational demands, Niche Mapper models were only run at high resolution with two GCMs – ACCESS 1.3 and HadGEM2-CC, with HadGEM2-CC selected because preliminary modelling indicated that it showed the greatest divergence from ACCESS 1.3 in regions currently occupied by koalas (Fig. S2). Downscaled projected monthly changes for 2070 were obtained as the differences from the base period (1990-2009) using SimCLIM (Yin *et al.*, 2013) (1km resolution) and assuming greenhouse gas concentrations for RCP8.5 and a moderate response to increased $CO_2$ concentrations (Riahi *et al.*, 2011). RCP 8.5 was selected as global greenhouse gas emissions have followed the most intensive emissions scenario (A1FI under the previous Special Report on Emission Scenarios) (Le Quere *et al.*, 2009).

At each site we splined predicted monthly changes in each variable to predict daily changes over an annual cycle, which were then applied to daily weather data for 1990-2009. Temperature and humidity values were adjusted by adding on the predicted change, while wind speed and cloud cover were adjusted using a proportional change factor (CSIRO and Bureau of Meterology, 2015) – an approach commonly used in impact assessments (Webb *et al.*, 2008, Bell *et al.*, 2012). To generate rainfall predictions we applied the monthly predicted changes in total precipitation to observed monthly rainfall values (1990-2009), with the constraint that monthly rainfall could not fall below 0. We then multiplied rainfall from all of the days with rainfall greater than 0 by a set proportion, such that the new monthly total rainfall matched predictions. This simple approach assumes that all rainy days are similarly affected however changes in the length of dry spells could occur if changes in rainfall resulted in days that were previously classified as ‘rainy days’ being classified as ‘dry days’ (i.e. if rainfall fell below 1 mm) and vice versa. Climate change may also alter the distribution of rainfall, resulting in intense rainfall events followed by longer runs of dry days. Spatial and regional predictions of how changes in variance are likely to influence patterns of daily weather and extremes were not available at the time of our study and therefore these types of changes are not captured in our simulated future weather datasets. Averages and extremes variables used in Maxent models were then generated for 2070 using this new 20-year daily time series.

Niche Mapper predictions and future climate layers were generated using a high-performance computing platform (‘Barcoo’ an IBM iDataplex x86 system with 1120 Intel Sandybridge compute cores running at 2.7GHz) administrated by the Victorian Life Sciences Computation Initiative.

### *Model evaluation & comparison*

To assess the predictive power of the Niche Mapper model we calculated AUC values (Swets, 1979) from the predicted habitat suitability score ($\bar{S}$) under the current climate for each koala observation location, as well as habitat suitability scores at 10,000 randomly distributed background points using the package pROC (Robin *et al.*, 2011). To test how well Niche Mapper captured temporal changes in habitat suitability, we also calculated AUC values using the mean of predicted habitat suitability for the year of the koala observation and the year prior ($n$ = 6472). Maxent models were assessed using 10-fold cross validation, with test AUC calculated as the mean of AUCs calculated from the predicted suitability scores at held-out ‘test’ presence locations in each fold, and 10,000 randomly distributed background points. AUC values were calculated using fitted (actual road density) and projected (assuming constant high road density) predictions.

Evaluating species distribution models against presence/absence data provides additional information about whether the model is over-predicting, as well as under-predicting (Guillera-Arroita *et al.*, 2015). Absence data were not readily available to evaluate the models, however we were able to generate absence data by assuming that koalas were absent from sites where other arboreal or semi-arboreal mammals were observed (i.e. we assumed that, if koalas were present at the site, they too would have been observed). These assumptions are likely to be most realistic for visual observations (e.g. spotlighting) in planned/systematic surveys, however we were unable to obtain information about the type of record from all states and so included all records. ‘Absence’ (non-observation) data derived in this way can be thought of as possessing reliability intermediate between randomly chosen pseudo-absence data and systematically recorded field absences. To minimise the risk of including false absence points within inhabited sites, we excluded absence points that were within 10km of koala presence observations (the maximum dispersal distance across a range of koala studies). This left 3285 absence points with which to evaluate the model (Fig. S3). Using this dataset we generated AUC values of all models using the package pROC (Robin *et al.*, 2011). Within this dataset, absence points were located primarily within the koala’s range, thus these values reflect the model’s ability to distinguish habitat used by koalas from habitat used by other arboreal mammals at relatively fine (~10km) scales.

We examined correlations between habitat suitability predicted by Niche Mapper and Maxent models across all time periods using Pearson’s correlation coefficients and quantile regression, as well as by visually assessing spatial patterns in predictions. We examined relationships with and without incorporating dynamic information about habitat suitability (e.g. suitability across sequential years) into Niche Mapper model predictions, since Maxent models produced a single (static) prediction of habitat suitability. We generated uncertainty maps by plotting the standard deviation of predicted habitat suitability for i) Maxent models varying predictor variables (averages, extremes A, extremes B) and GCM, ii) Niche Mapper varying foliage water content (low, med, high, predict) and GCM. We also produced a combined uncertainty map after re-scaling Niche Mapper predictions by multiplying by the maximum habitat suitability predicted by Maxent models under the current climate (0.7).

## Results

The Niche Mapper model had high predictive power when tested against independently collected presence data (Fig. 1a), with an AUC of 0.868 (95% CI: 0.861-0.874). Our simulations suggest that the key process limiting distributions is the ability of koalas to meet their weekly water requirements. Whether koalas are predicted to be able to survive and reproduce in regions that impose high water loss rates is influenced strongly by the timing of rainfall and by leaf water content. In particular, obtaining free water from the environment (by eating wet leaves or drinking) means that koalas could meet their water requirements when they could not acquire sufficient water from food intake alone due to intake constraints. Consistent with this, simulations indicate that predicted inland range-limits are dynamic, showing considerable inter-annual variation, driven by the timing of rainfall relative to thermally stressful conditions (Fig. S4). These temporal trends were reflected in presence data, with higher AUC values when habitat suitability was calculated using the years prior to, and of, the observation, rather than the mean across all years (AUC = 0.887, 95% CI: 0.884-0.890). In southern inland regions, some sites were predicted to be unsuitable for reproducing females for one generation or more, despite moderate habitat suitability across the 20 year period (Fig. 2).

In the averages Maxent model (Fig. 1b), predicted habitat suitability decreased markedly in regions with mean maximum monthly temperatures greater than 37°C and annual rainfall less than 600mm. Habitat suitability was also lower where Eucalyptus forest or woodland comprised less than 10% or more than 80% of the cell, although this variable had low relative contribution (4.2%) to the model. Predicted habitat suitability from the two extremes models was very similar under the current climate (Fig. 1c,d). Both models had average test AUC values of 0.908 ±0.009 and response curves showed very similar patterns, although variable contributions to the model differed (Table 1, Fig. S5). In both models, habitat suitability decreased in regions with maximum runs of dry days greater than 35 and very high or low vapour pressure during hot weather. Habitat suitability was again lower where Eucalyptus forest or woodland comprised less than 10% of the cell, but this variable made a slightly higher (8-9%) contribution to the models. In extremes model A, habitat suitability declined in regions with 95th percentile temperatures > 32°C with a sharp decline >39°C, while in extremes model B, habitat suitability declined sharply in regions with maximum runs of hot, dry days greater than 7.5 days. The fitted responses for all Maxent models showed declining frequency of observed presence with low road density, most likely reflecting the absence of sampling in more remote areas. To factor out this sampling bias we predicted distributions under current and future climates to a constant road density (i.e. constant sampling effort, *sensu* Leathwick *et al.*, 2006, Warton *et al.* 2013). Model AUC values were calculated using both fitted and projected (i.e. assuming constant high sampling) layers. Models fit using a sample bias grid in Maxent (an alternative approach for dealing with bias) showed very similar spatial predictions and model performance (Supporting Information, Fig S1a-f), while models that did not account for sampling bias predicted slightly lower habitat suitability in some regions of inland and northern Australia (Fig S1g-i).

Maxent models had slightly higher predictive ability than the Niche Mapper model, with test AUC values calculated using presence-background data ranging from 0.894 – 0.908 (Table 1). When assessed using presence-‘absence’ data generated using records of other arboreal mammals, all models had lower predictive power, however the Maxent models, particularly extremes model B, were much better at identifying koala habitat (Table 1).

### ***Predictions & sources of uncertainty***

Under the current climate, Niche Mapper predictions of koala habitat suitability were most strongly correlated with the two Maxent models based on weather as opposed to climate variables (Table 2), although there was a positive correlation ($r > 0.7$) between all four sets of predictions. Quantile regression (5th, 50th and 95th percentiles) illustrated that the Maxent models that included weather show strong agreement with Niche Mapper in regions that Niche Mapper predicts to have low mean habitat suitability (all intercepts < 0.1), with greater divergence in regions Niche Mapper predicted to be highly suitable (95th percentile slopes: 0.64 and 0.58, 5th percentile slopes: 0.12 and 0.1, Fig. 3). This is likely because Niche Mapper has no information about the presence of Eucalyptus trees (Fig. 2b). When we constrained the Niche Mapper output so that sites that were predicted to be unsuitable for one generation had a suitability of 0, the agreement between models weakened. This indicates that at least some of these sites that were reclassified had moderate values of habitat suitability when temporal trends in poor years were not considered. There was a weaker relationship between habitat suitability predicted by the averages Maxent model and Niche Mapper (Table 2), with less agreement regarding which areas were unsuitable (95th percentile intercept = 0.32, Fig. 3). Most notably, the Maxent averages model predicted moderately high habitat suitability in some regions of northern Australia that were predicted to be unsuitable by Niche Mapper (Fig. 2).

Under future climate scenarios (ACCESS 1.3), all models predicted a range contraction towards the coast, with all Maxent models also predicting that regions of high habitat suitability will be concentrated in the south (Fig 2). Future predictions from the mechanistic model showed the strongest agreement with Maxent model extremes A ($r = 0.85$, Table 2). Despite having very similar predictions under the current climate (Fig 1) the Maxent models based on weather extremes made quite different predictions under climate change, with Maxent extremes B predicting a much more rapid and severe decline in northern regions, including coastal populations (Fig. 1).

MESS maps (Multivariate Environmental Similarity Surfaces, Elith *et al.*, 2010), indicated that Maxent B was extrapolating in these northern regions, with much longer runs of hot, dry days than observed under the current climate (Fig. S6). The Maxent model based on climate averages showed slightly higher agreement with Niche Mapper predictions in the future (2070), with regions of northern Australia now projected to be unsuitable by both models. The averages model predicted declines in habitat suitability across regions of southern Australia that were predicted to be relatively unaffected by climate change by Niche Mapper and the weather Maxent models (Fig. 1).

Prediction uncertainty across Maxent models was highest in northern Australia under the current climate, but shifted to be concentrated along the northern coastal region and south-eastern Australia by 2070 (Fig. 4). Changes in simulated water content of leaves strongly influenced Niche Mapper predictions across inland regions under both current and future climates. Under projected 2070 climates, only southern coastal regions had both high mean predicted habitat suitability and low prediction uncertainty across all models (due to GCM, differences in leaf water content and predictor variables). Climate refugia for 2070 predicted with high confidence (moderate-high habitat suitability across all models and scenarios) were located along coastal areas in southern Victoria, South Australia and southern NSW, as well as the NSW north coast, and New England Tablelands (Fig. 4d). While there was strong agreement about the loss of suitable habitat in northern inland regions across all models, predictions regarding the location and quality of habitat in northern Australia differed (Fig. 4c). Locations of potential refugia in north-eastern Australia (Fig. 4d) were strongly driven by NicheMapper predictions of habitat suitability assuming low foliage water content (i.e. under the most pessimistic circumstances). Prediction uncertainty for Maxent models using all six GCMs was similar to prediction uncertainty using ACCESS 1.3 and HadGEM2-CC ($r$ = 0.973, Fig. S7). The effect of GCM on predicted habitat suitability varied between models and regions, with ACCESS 1.3 associated with lower predicted habitat suitability in northern regions for all models excluding Maxent extremes B, and higher habitat suitability in south-west areas of the modelled region for Niche Mapper and to a lesser extent, the Maxent extremes models (Fig. S8). Across the modelled region, predictor variables (simulated water content, selected environmental variables) were a greater source of uncertainty than the choice of GCM.

## Discussion

Climate change has multiple dimensions spanning both time and space (Garcia *et al.*, 2014) yet climate change forecasts based on correlative SDMs have predominantly characterized species responses to climate averages, paying much less attention to climate extremes or the timing of climate events (Helmuth *et al.*, 2014). Our results indicate that the timing of thermally stressful conditions relative to water availability (recent rainfall and foliage water content) is an important driver of koala distributions and will strongly determine the locations of climate and weather refugia in the coming decades. Thermally stressful conditions coupled with low water availability are likely to be an important determinant of the future distributions of a range of taxa (Kearney *et al.*, 2010, Krockenberger *et al.*, 2012) and our results suggest that explicitly modelling these, and related extreme conditions, could improve the predictive power of correlative species distribution models.

Predictions generated using correlative and process-explicit models rely on very different assumptions and can capture different processes (Dormann *et al.*, 2012). They can therefore be viewed as independent lines of evidence, with congruent forecasts viewed as more likely (Morin & Thuiller, 2009, Kearney *et al.*, 2010). In our study, both Niche Mapper and Maxent simulation sets identified coastal regions of southern and south-eastern Australia as climate refugia for koalas and predicted the loss of inland northern inland populations by 2070. These predictions were consistent across different modelling approaches, GCMs and predictor variables, providing a sound basis for conservation decisions about how to manage these particular regions. These refugial areas were largely *in situ* (falling within the koala's current range), although additional *ex situ* climate refugia may exist in regions not considered in this study because they are inaccessible due to dispersal barriers (e.g. Tasmania). Results from the biophysical model also provide insight into the types of habitat that may provide important refuges for koalas at finer scales within marginal inland and northern regions that are expected to become increasingly unsuitable (e.g. Fig. 4d). Habitats where koalas have access to cooler microclimates (e.g. due to fine-scale topographic relief), and either free water or high foliage water content, can help buffer koalas against heat-related mortality during extreme years (Gordon *et al.*, 1988). Such refuges are likely to become increasingly important for the persistence of many inland populations in the coming decades, both in marginal regions and areas that show considerable inter-annual variability (e.g. Fig 2c).

Despite the fact that all SDM predictor sets used in our study were designed to capture the same process (heat stress and water availability), the predicted impact of climate change on koalas differed considerably between models. Our analyses suggest that the commonly adopted process of removing variables that are correlated under the current climate could strongly influence future predictions because variable sets that are interchangeable under current conditions can diverge in the future (e.g. T95 and length of heat events, Table S2).

Consistent with a number of previous studies, we also found that models with different variable sets had similar predictive power as measured by AUC (a widely used metric) under the current climate, yet produced very different forecasts of species responses to climate change (Elith *et al.*, 2010, Synes & Osborne, 2011). The problems associated with projecting to new environments with different correlation structure have been highlighted by studies examining collinearity (Dormann *et al.*, 2013). However, discussions have largely focused on statistical approaches that can be used to identify and help reduce the impacts of collinearity, with less focus on how to select predictor variables (although see Barbet-Massin & Jetz, 2014).

Interrogating and comparing predictions from different modelling approaches is one way to gain insight into the strengths and weaknesses of different approaches (Guisan & Zimmermann, 2000, Elith & Graham, 2009), why predictions differ, and what processes are (and are not) being captured by individual models (Elith *et al.*, 2010). For example, the averages model overestimates habitat suitability in northern Australia compared with the mechanistic model and the two weather-based correlative models (Fig. 1,2a). Across this northern region, annual rainfall and maximum temperatures alone are poor predictors of whether koalas are likely to be able to meet their water requirements. This is because periods of high water requirements coincide with a prolonged dry season, and high vapour pressure during hot weather may also reduce the effectiveness of evaporative cooling. The limits of the mechanistic model are also evident from this comparison; information about whether koalas can meet their energy and water requirements provides a strong basis for predicting koala distribution limits but not for discriminating between habitat utilized by koalas and other arboreal mammals at finer scales within climatically suitable regions. Niche Mapper does not use information about the availability of Eucalyptus trees, or where koalas are currently found in the landscape (which reflects where food trees are available), and consequently predicts some regions to be highly suitable that do not contain suitable koala habitat (i.e. food trees). The usefulness and robustness of a particular model is heavily influenced by the aim and scale of the study (Guisan *et al.*, 2013). For example, the ability to identify climatically suitable regions not currently inhabited by the species can be a strength of mechanistic approaches (e.g. when identifying translocation sites for species with restricted ranges – (Mitchell *et al.*, 2013)). However, integrating Niche Mapper predictions with land-use data will be necessary for many management decisions, including where to conserve existing koala habitat.

We assume that the availability of Eucalyptus trees remains constant to 2070 and beyond, providing food and shelter throughout the period. This may not be the case (Adams-Hosking *et al.* 2012, Butt *et al.* 2013). Our results suggest that even if Eucalyptus habitat remains available, changes in climate are likely to lead to the loss of koala populations in inland northern regions. However, the contraction and fragmentation of koala food tree distributions may exacerbate koala range retraction, and will be a key concern when managing climate change refugia (Adams-Hosking *et al.* 2012).

Our analyses suggest that the inclusion of weather variables that reflect physiologically stressful conditions, such as the maximum length of dry spells, could improve SDM forecasts. However, adequately characterizing physiologically stressful 'extreme' conditions for species is not straightforward (Helmuth *et al.*, 2014). Extremes are typically defined statistically (e.g. as those with ≤5% statistical probability of occurrence) with reference to a base climate (Meehl *et al.*, 2000, Smith, 2011). In our study, discrepancies between future predictions from the two extremes models were largely driven by the fact that in more stable northern environments, higher maximum temperatures have a disproportionate effect on the length of sequential days with temperatures in the 90th percentile, with these longer heat events leading to low predicted habitat suitability across northern regions (Fig. 2d). The biophysical model predicted that, in at least some of these northern regions, koalas would be able to meet their water requirements during these longer heat events. But this inference is dependent on the availability of suitable foliage (which may be affected by extended dry hot weather) and does not account for other potential fitness consequences, such as trade-offs between foraging and behavioural thermoregulation (du Plessis *et al.*, 2012), which are not captured by the model. Where biological data is available, the use of species-specific thresholds to define extreme events is an alternative approach that could be used to define extreme conditions for species that do not show geographic variation in these traits (Smith, 2011).

Niche Mapper predictions were sensitive to simulated foliage water content, which influences how easily koalas can meet their water requirements. Landscape-level data on foliage water content across seasons is not available for koala food trees, and leaf properties and intake constraints may also change in the future due to the combined effect of higher $CO_2$ concentrations and changes in climate (Lawler *et al.*, 1997). Koalas are likely to be particularly sensitive to such changes (Lunney *et al.*, 2012). By predicting koala responses across a range of foliage water content values, we were able to identify where model predictions are most sensitive to this parameter (and thus where data collection would be yield the biggest reduction in model uncertainty) as well as where management actions directed at increasing foliage water available to koalas could be most effective. This ability to explore how changes in key parameters influence predicted distribution limits is one of the strengths of mechanistic modelling approaches (Kearney *et al.*, 2009).

Body size and fur properties can also influence climate sensitivity and predicted habitat suitability in koalas and were estimated from museum data in our study (Briscoe *et al.*, 2015). While we assumed that trait distributions remain constant through time, clines in traits may shift in response to climate change (Gardner *et al.*, 2009), potentially reducing koala population vulnerability.

Future koala distributions will also be influenced by variation in habitat suitability. Rather than representing model uncertainty, the inter-annual variation in habitat suitability predicted by Niche Mapper reflects the dynamic nature of habitat suitability within inland regions and is consistent with studies showing that koalas are more broadly distributed during favourable conditions in these regions but contract during drought (Seabrook *et al.*, 2011). However, poor years may have disproportionate effects on population dynamics (Altwegg *et al.*, 2006, Frederiksen *et al.*, 2008), and demographic processes including dispersal are likely to modify the relationship between predicted habitat suitability and long-term population persistence (Johst *et al.*, 2002). Where sufficient data are available, predictions of weather impacts on individuals could be translated into estimates of long-term population persistence using a meta-population framework (Bennie *et al.*, 2013), a promising avenue for future research.

To be useful for conservation, species distribution models need to identify refugia where populations are most likely to persist – which may be different to identifying regions that are suitable on average (Keppel *et al.*, 2015). We should also have high confidence in predicted refugia in that they should be robust to potential sources of uncertainty and extreme events, especially if they become relatively isolated and difficult to recolonize. Characterising and quantifying model uncertainty allows explicit consideration of uncertainty in conservation decisions (Diniz-Filho *et al.*, 2009, Kujala *et al.*, 2013). However, we suggest that effort also needs to be directed at reducing uncertainty by improving our understanding of the processes that limit species distributions. Combining biophysical modelling approaches, that do not rely on correlations between variables and so are more likely to perform similarly under current and future climates (Dormann *et al.*, 2012), with statistical ecological approaches is one way to improve the quality and certainty of refugia predictions.

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## Supporting Information

Table S1: Key physiological, morphological and behavioural parameters used in the koala Niche Mapper model

Table S2: Correlations between environmental variables used in Maxent models under current and future climates.

Figure S1: Effect of approaches used to account for sampling bias on model predictions

Figure S2: Effect of GCM on Niche Mapper predictions of koala habitat suitability in 2070.

Figure S3: Presence and ‘absence’ points used to evaluate koala distribution models.

Figure S4: Yearly Niche Mapper predictions of koala habitat suitability across eastern Australia (1990-2009).

Figure S5: Marginal response curves for Maxent models.

Figure S6: MESS maps of Maxent predictions showing regions of extrapolation.

Figure S7: Maxent model prediction uncertainty due to predictor variables and GCMs.

Figure S8: Difference in predicted habitat suitability for koalas in 2070 across models due to general circulation model.

## Figure captions

Figure 1. Predicted habitat suitability for koalas under current and 2070 climates as predicted by a) Niche Mapper, b) Maxent with long-term climate averages, c) Maxent with weather extremes A, d) Maxent with weather extremes B, as well as the predicted change in habitat suitability from current to 2070 for each model (bottom). Koala distribution records are shown in the insert. All models predicted a substantial decline in suitable habitat in central and northern inland regions by 2070. The averages and extremes B Maxent models also predicted reduced habitat suitability in some parts of southern Australia, and the extremes B model predicted a more severe decline in central and northern coastal regions than other models. Note the divergence of the two extremes models, which show high agreement under the current climate.

Figure 2. Differences in predicted habitat suitability predicted by Niche Mapper and a,d) Maxent averages model, b,e) Maxent extremes A, c,f) Maxent extremes B under current climate (a-c) and 2070 climate (d-f). Positive values (purple) correspond with regions where Niche Mapper had higher predicted habitat suitability than Maxent models. To allow comparison, Niche Mapper predictions were rescaled so that the maximum predicted habitat suitability value was equal to the maximum value predicted by Maxent.

Figure 3. The relationship between habitat suitability predicted by Niche Mapper (x-axis) and the three Maxent models (y-axis) under current climate. Niche Mapper habitat suitability was calculated as the mean across all 20 years (top) or the mean across all years with the additional constraint that sites with 5 sequential poor years were classified as unsuitable

(bottom). Lines represent 5th (lower), 50th (middle) and 95th(upper) quantile regressions. The two extremes models showed good agreement with Niche Mapper in regions that Niche Mapper predicted to have low mean habitat suitability, but diverged in regions Niche Mapper predicted to be more suitable. The relationship between the averages model and Niche Mapper is much noisier, as indicated by the flatter 5th and 95th quantile regression lines. Classifying sites with sequential poor years as unsuitable reduced the agreement between NicheMapper and the extremes Maxent model predictions.

Figure 4. Mean and standard deviation of predicted habitat suitabilty for koalas across eastern Australia under the current climate and 2070 using a) Maxent models, b) Niche Mapper models, c) all models (2070 only), and d) minimum habitat suitability across all models in 2070. To allow comparison, Niche Mapper predictions were rescaled so that the maximum predicted habitat suitability value was equal to the maximum value predicted by Maxent. Mean and standard deviations were calculated from predictions using two GCMs (ACCESS 1.3 and HadGEM2-CC) as well as varying predictor variables (Maxent) or foliage water content (Niche Mapper). Location of refugia (d) were strongly driven by NicheMapper predictions of habitat suitability assuming low foliage water content (i.e. under the most pessimistic circumstances). In northern Australia (d-insert) refugia are typically high elevation sites.

## Tables

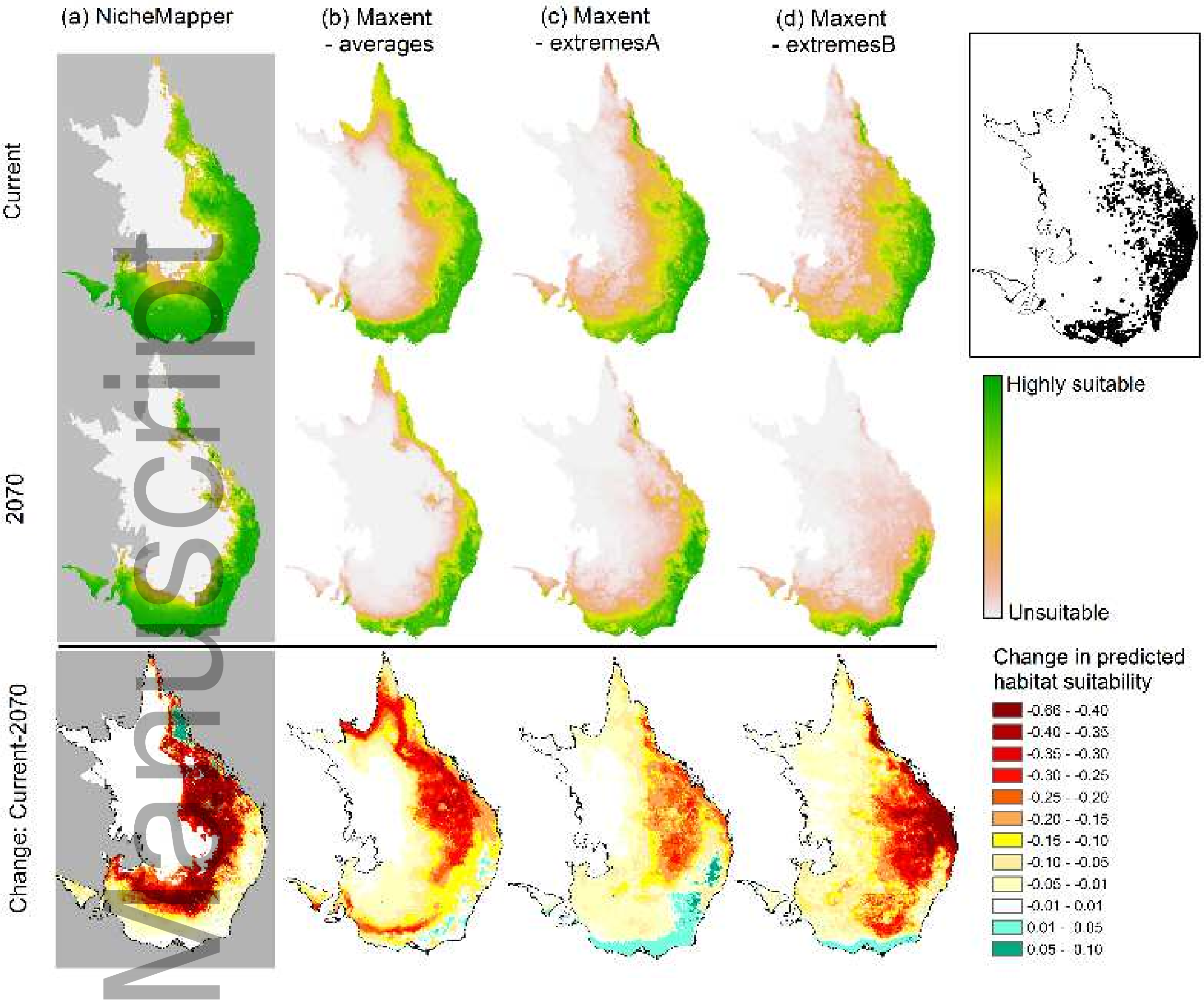
Table 1. Model information including variables, variable importance and AUC values of models used to predict koala distributions across Eastern Australia. AUC values were calculated using both presence-background and presence-‘absence’ data, and using either fitted or projected (i.e. assuming constant road density) model predictions (Maxent models only).

| Model | Variables | Permutation importance | AUC – background | | AUC –‘absence’ | |
|---|---|---|---|---|---|---|
| | | | fitted | projected | fitted | projected |
| Niche Mapper | Reproducing females with site-specific morphology | NA | 0.868 | | 0.557 | |
| Maxent - Average climate | 1) Annual rainfall | 36.9 | 0.894 | 0.888 | 0.655 | 0.649 |
| | 2) Maximum temperature in the warmest period (month) | 48.5 | | | | |
| | 3) *Eucalyptus* forest/woodland cover | 4.2 | | | | |
| | 4) Road density | 10.4 | | | | |
| Maxent - Extreme weather A | 1) Maximum run of dry days | 39.7 | 0.908 | 0.903 | 0.697 | 0.706 |
| | 2) T95 (95th percentile temperature) | 35.4 | | | | |
| | 3) Vapour pressure during hot weather | 12.0 | | | | |
| | 4) Eucalyptus forest/woodland cover | 7.6 | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 5) Road density | 5.3 | | | | |
| Maxent - Extreme weather B | 6) Maximum run of dry days | 70.4 | 0.908 | 0.904 | 0.718 | 0.720 |
| | 7) Maximum run of hot days | 5.9 | | | | |
| | 8) Vapour pressure during hot weather | 9.8 | | | | |
| | 9) Eucalyptus forest/woodland cover | 9.4 | | | | |
| | 10) Road density | 4.5 | | | | |

Table 2: Pearson's correlation coefficients (*r*) for habitat suitability predictions of models under current (top) and 2070 (ACCESS 1.3, bottom) climates (correlations based on 100,000 points randomly distributed across the study area).

| Model | Niche Mapper | Maxent – averages | Maxent – extA | Maxent – extB |
|---|---|---|---|---|
| Niche Mapper | | 0.72 | 0.83 | 0.78 |
| Maxent – averages | 0.78 | | 0.87 | 0.81 |
| Maxent – extA | 0.85 | 0.91 | | 0.98 |
| Maxent – extB | 0.77 | 0.78 | 0.90 | |



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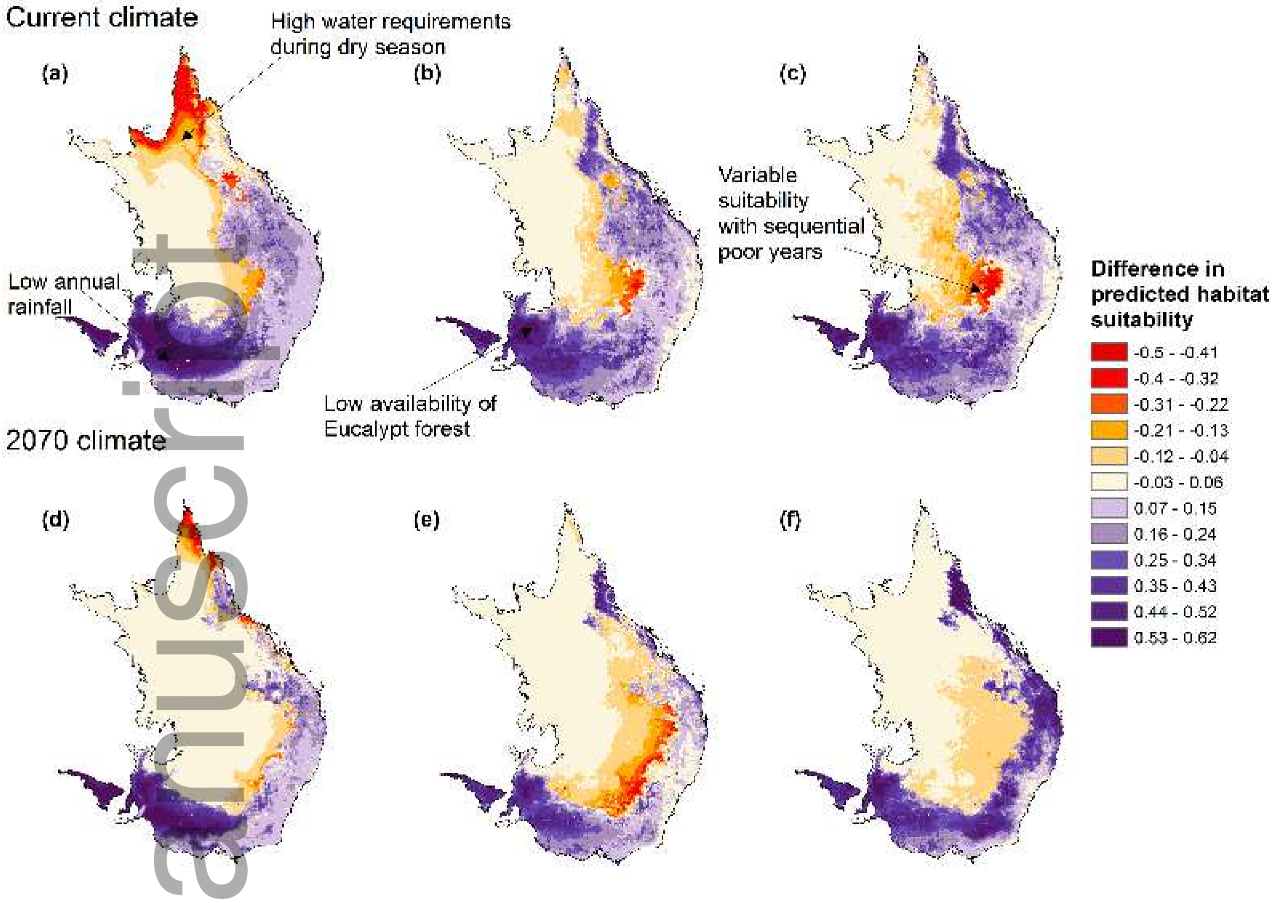

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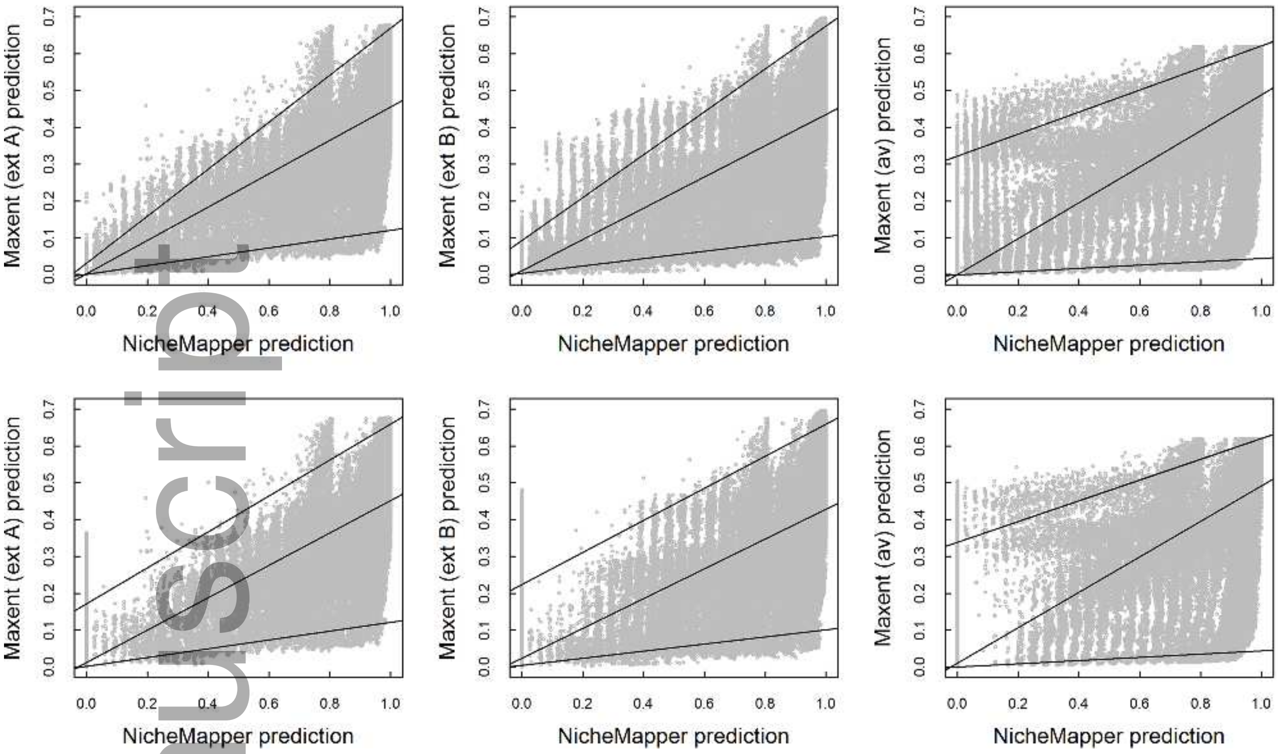

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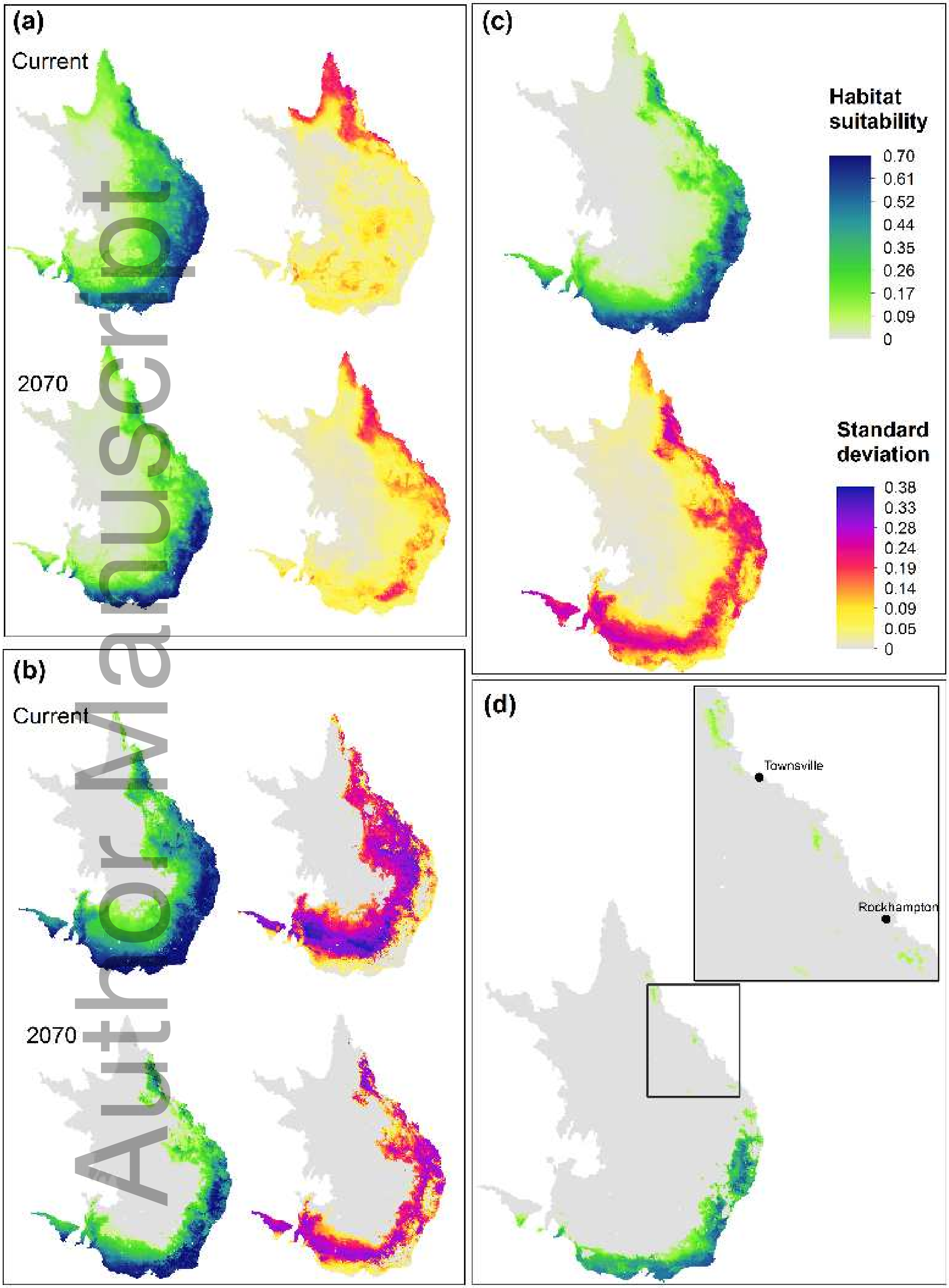

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