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Modelling climate-change-induced shifts in the distribution of the koala

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Abstract

Context. The impacts of climate change on the climate envelopes, and hence, distributions of species, are of ongoing concern for biodiversity worldwide. Knowing where climate refuge habitats will occur in the future is essential to conservation planning. The koala (*Phascolarctos cinereus*) is recognised by the International Union for Conservation of Nature (IUCN) as a species highly vulnerable to climate change. However, the impact of climate change on its distribution is poorly understood.

Aims. We aimed to predict the likely shifts in the climate envelope of the koala throughout its natural distribution under various climate change scenarios and identify potential future climate refugia.

Methods. To predict possible future koala climate envelopes we developed bioclimatic models using Maxent, based on a substantial database of locality records and several climate change scenarios.

Key results. The predicted current koala climate envelope was concentrated in south-east Queensland, eastern New South Wales and eastern Victoria, which generally showed congruency with their current known distribution. Under realistic projected future climate change, with the climate becoming increasingly drier and warmer, the models showed a significant progressive eastward and southward contraction in the koala's climate envelope limit in Queensland, New South Wales and Victoria. The models also indicated novel potentially suitable climate habitat in Tasmania and south-western Australia.

Conclusions. Under a future hotter and drier climate, current koala distributions, based on their climate envelope, will likely contract eastwards and southwards to many regions where koala populations are declining due to additional threats of high human population densities and ongoing pressures from habitat loss, dog attacks and vehicle collisions. In arid and semi-arid regions such as the Mulgalands of south-western Queensland, climate change is likely to compound the impacts of habitat loss, resulting in significant contractions in the distribution of this species.

Implications. Climate change pressures will likely change priorities for allocating conservation efforts for many species. Conservation planning needs to identify areas that will provide climatically suitable habitat for a species in a changing climate. In the case of the koala, inland habitats are likely to become climatically unsuitable, increasing the need to protect and restore the more mesic habitats, which are under threat from urbanisation. National and regional koala conservation policies need to anticipate these changes and synergistic threats. Therefore, a proactive approach to conservation planning is necessary to protect the koala and other species that depend on eucalypt forests.

Additional keywords: Australia, climate envelope, climate refuge habitats, Maxent, synergistic threats.

Introduction

Most ecosystems worldwide continue to be threatened by global climate change, as the distributions of suitable habitat for species become altered (Williams and Jackson 2007; Fitzpatrick *et al*. 2008). Global temperatures have been increasing over the past 50 years, combined with more frequent hot days and nights and increased rainfall variability (IPCC 2007). Anthropogenic climate change is expected to lead to further increases in climate extremes (Allison *et al.* 2009). It is therefore important to understand the distributional shifts in species in response to ongoing climate change.

The identification of 'climatic refuge habitats' is an important task for conservation planning in a changing climate (IPCC 2007). From an evolutionary perspective, the term 'refugia' refers to core regions where organisms are able to persist during a time of change in climatic and environmental conditions and when their wider geographic distribution becomes uninhabitable (Byrne 2008). For example, Hardy *et al*. (2010)

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argue that sites at higher altitudes can provide refuges for phytophagous insects when their lower ranges are subject to extreme climatic events and Gibson *et al*. (2010) suggest that conservation efforts should concentrate on identifying and protecting refuges where quokkas (*Setonix brachyurus*) are predicted to persist over time with climate change.

In Australia, climate change due to increased anthropogenic greenhouse gases, coupled with land surface feedbacks from land clearing, appears to be amplifying natural climatic variability, especially in south-eastern Australia (CSIRO 2007; McAlpine *et al*. 2009; Steffen 2009). This has the potential to tip the region's climate into a new regime of more frequent and severe droughts, with adverse consequences for native ecosystems and their biodiversity, particularly because of its rapidity (McAlpine *et al*. 2009; Lindenmayer *et al*. 2010). The catastrophic bushfires of 2009 in Victoria in southern Australia that followed an unprecedented heatwave (BOM 2009) may have been early warning signs that such climate changes are already occurring.

Species distribution models based on current ecological niche constraints are useful for projecting future species distributions (Wiens *et al*. 2009). Such predictive models in general are correlative in their approach and use either statistical techniques (Thuiller *et al*. 2004) or machine learning approaches (Peterson *et al*. 2002). They are founded on ecological niche theory (Hutchinson 1957), which describes the fundamental and realised niches in which species can exist. There are well recognised limitations to correlative approaches, such as underlying assumptions that are made, for example, about biotic interactions and dispersal ability that affect the distributions of species (Wiens *et al*. 2009). Despite these limitations, correlative models currently provide a suitable approach for predicting climate-induced shifts in species' distributions without knowing species' physiological and evolutionary responses to climate change (Pearson *et al*. 2002; Lawler *et al*. 2006).

The koala (*Phascolarctos cinereus*) is a wide-ranging endemic Australian folivorous marsupial whose habitat quality is closely associated with a relatively small number of *Eucalyptus* species, which provide nutrient-rich foliage (Moore and Foley 2005). Koalas are highly sensitive to habitat loss and fragmentation (McAlpine *et al*. 2006; Rhodes *et al*. 2008) as indicated in a recent population decline of 51% in less than three years in a rapidly urbanising region of south-eastern Queensland, Australia (DERM 2009). The threat to koalas from climatic extremes has also been observed, with past population collapses such as during 1979–80, when 63% of a koala population within south-western Queensland died after a drought and heatwave (including 12 consecutive days when the temperature exceeded 40°C) (Gordon *et al*. 1988). Furthermore, the International Union for Conservation of Nature (IUCN 2009) states that koalas have a very limited capability to adapt to rapid human-induced climate change. The climate envelope of a species can be defined as the predicted potential distribution of a species on the basis of bioclimate (Nix 1986). If the current climate envelope of koalas contracts under predicted climate change, this species will be highly susceptible to further local and regional extinctions, especially with the combined effects of climate change, habitat degradation, fragmentation and loss, and disease (e.g. McInnes *et al*. 2009; Mitchell *et al*. 2009). The synergistic effects of multiple threats to biodiversity are receiving increasing attention worldwide, for example Luck (2007), Sodhi *et al*. (2008), Kleijn *et al*. (2009) and Giam *et al*. (2010), and is likely to be an important consideration for the conservation of the koala.

The primary aim of this study was to model the current and future climate envelope of koalas throughout eastern Australia under projected changes in climate. By applying Maxent (Phillips *et al*. 2004) we aimed to provide conservation managers and decision makers with a robust guide to likely shifts in koala distribution by identifying potential future climate refuge regions for koalas under a warmer and drier climate.

Materials and methods

Study area

The study area was in the eastern region of the Australian continent. Koalas are currently distributed in Queensland (QLD), New South Wales (NSW), South Australia (SA), Victoria (VIC) and various off-shore islands. They also occur on an enclosed reserve in Western Australia (WA). This study focussed on the current climate envelope of koalas in QLD, NSW and VIC (Fig. 1). We excluded the island, SA and WA koala populations from the analysis to concentrate on areas containing the most natural populations. We defined 'natural' as populations that are not derived primarily from translocated or introduced individuals, although we recognise that some island populations may be natural (e.g. Woodward *et al*. 2008).

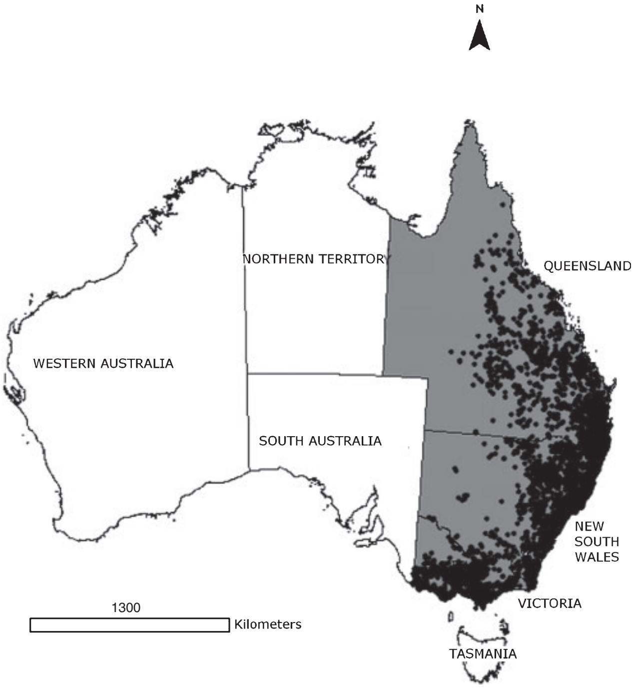

Fig. 1. The studied states of Queensland, New South Wales and Victoria shaded in grey with koala records in black. Sources of modern koala records data: Queensland DERM (2008); New South Wales DECC (2008); and Victorian DSE (2008).

Koala occurrence data

Koala occurrence data consisted of both incidental observations and various systematic surveys and were obtained from relevant government agency databases. These were the QLD Department of Environment and Resource Management, the NSW Department of Environment, Climate Change and Water and the Victorian Department of Sustainability and Environment. Historical as well as contemporary records were included to ensure that all climatic conditions in which modern koalas are known to have occurred over this period were accounted for. These records incorporated approximately the past 100 years. Duplicate records, as well as obvious outliers indicating data entry mistakes were removed manually. To reduce the possibility of geographical bias, such as a high density of records collected in highly populated areas, records were filtered using a method described by McKenney *et al*. (2007). Records were overlaid with a 10 km grid and then one record was randomly selected from each grid. This reduced the total number of occurrence records for the model development from 32 029 to 3 315.

Climate data

We used baseline (1961–90) gridded climate data of mean maximum summer temperatures and mean annual rainfall (BOM 2003) to model the current climate envelope of koalas. We chose these two parameters for our current and future predictions because heat and drought are found to be key drivers of koala distributions (e.g. Gordon *et al*. 1988; Ellis *et al*. 2010). Additionally, average annual precipitation and mean temperature of the warmest month were found to be much more important than any other factors in predicting vegetation occurrence (Box 1981). These findings concord with Hughes *et al*. (1996) who predict that with warming of 5°C, 73% of Australian *Eucalyptus* species, the key food source for koalas, would be displaced from their present geographic distribution. To predict future koala climate envelopes, we used the CSIRO MK 3.5 climate model scenarios of mean maximum summer temperatures and mean annual rainfall for 2030, 2050 and 2070 derived from OzClim (CSIRO 2010). Anthropogenic climate change may be more rapid and widespread than predicted by the IPCC AR4 (Raupach *et al*. 2008) and global CO_2 emissions from fossil fuel burning are tracking near the highest scenarios considered so far by the IPCC (Allison *et al*. 2009). We therefore selected the SRES A1FI high emission scenario group that describes a future of rapid economic growth, a global population that peaks in mid-century, and a continuation of high energy needs being met by fossil fuel sources (CSIRO 2010).

Maxent

We chose Maxent for our modelling because it can use presence only data, can utilise both continuous and categorical data (Phillips *et al*. 2004) and has been found to be a robust modelling technique (e.g. Elith *et al*. 2006; Elith and Graham 2009). Maxent uses a deterministic algorithm to converge to the optimal (maximum entropy) probability distribution of a species (Phillips *et al*. 2006). It trains the model by starting from the uniform distribution and repeatedly improving to fit the data. Other environmental factors influencing koala distribution such as topography, soils and vegetation (Crowther *et al*. 2009) were not included, as the focus was on climate. We imported regional climate change patterns in ASCII grid format from the OzClim climate change scenarios and projected these future climate conditions onto the baseline climate fitted Maxent model that we developed at a 10 km^2 resolution. The model was built (trained) using 500 iterations on 75% of the koala occurrence data and the remaining 25% were randomly selected to test the model's predictive power. The model was evaluated using the area under the receiver operating characteristic (ROC) curve (AUC) and we employed bootstrapping ($n = 100$) to cross-validate the model.

Results

Fitted model – current climate envelope

The highest probabilities of predicted koala occurrences were in eastern Australia and were highly congruent with the current koala geographic distribution. High probabilities of koala occurrence were also predicted in areas of WA, SA and Tasmania, with lower probabilities predicted in far northern Australia (Fig. 2*a*). The response curves indicated that the highest probability of koala presence occurs between mean maximum summer temperatures of 23 and 26°C (Fig. 3*a*) and mean annual rainfall of between 700 and 1500 mm (Fig. 3*b*). These variables were found to be moderately negatively correlated ($r = -0.512$). The AUC over 100 replicates was 0.860 for the training data and 0.841 for the test data (random = 0.5). Mean training AUC derived from the 100 bootstraps was 0.858 (s.d. = 0.002) (Fig. 4). The averaged analysis of omission/commission showed a close fit of the training omission rate and predicted area as a function of the cumulative threshold, indicating high confidence in the model's discrimination ability. The jackknife test of variable importance indicated that the environmental variable during the Maxent training with highest gain was mean maximum summer temperature (Fig. 5*a*), which also decreased the gain the most when it was omitted; suggesting that this variable has the most important information. When using the koala records set aside for testing the model (25%), mean maximum summer temperature was again the most important variable (Fig. 5*b*).

Future climate envelopes

When projecting the future climate change scenarios onto the fitted model, there were progressive eastward climate envelope contractions by 2030, particularly in the areas of highest probability in QLD and NSW (Fig. 2*b*). By 2050 and 2070, these contractions became increasingly pronounced and shifted southwards, with the highest probabilities of koala presence restricted to patches of eastern NSW, eastern VIC and Tasmania (Fig. 2*c*, *d*). These predictions represent significant progressive contractions from the present distribution of koalas (Fig. 1) in the western regions of QLD, NSW and western VIC by 2050.

Discussion

This study provides robust evidence for the first time of the magnitude of projected changes in mean climate on the future geographic climate envelope of the koala. Under a projected

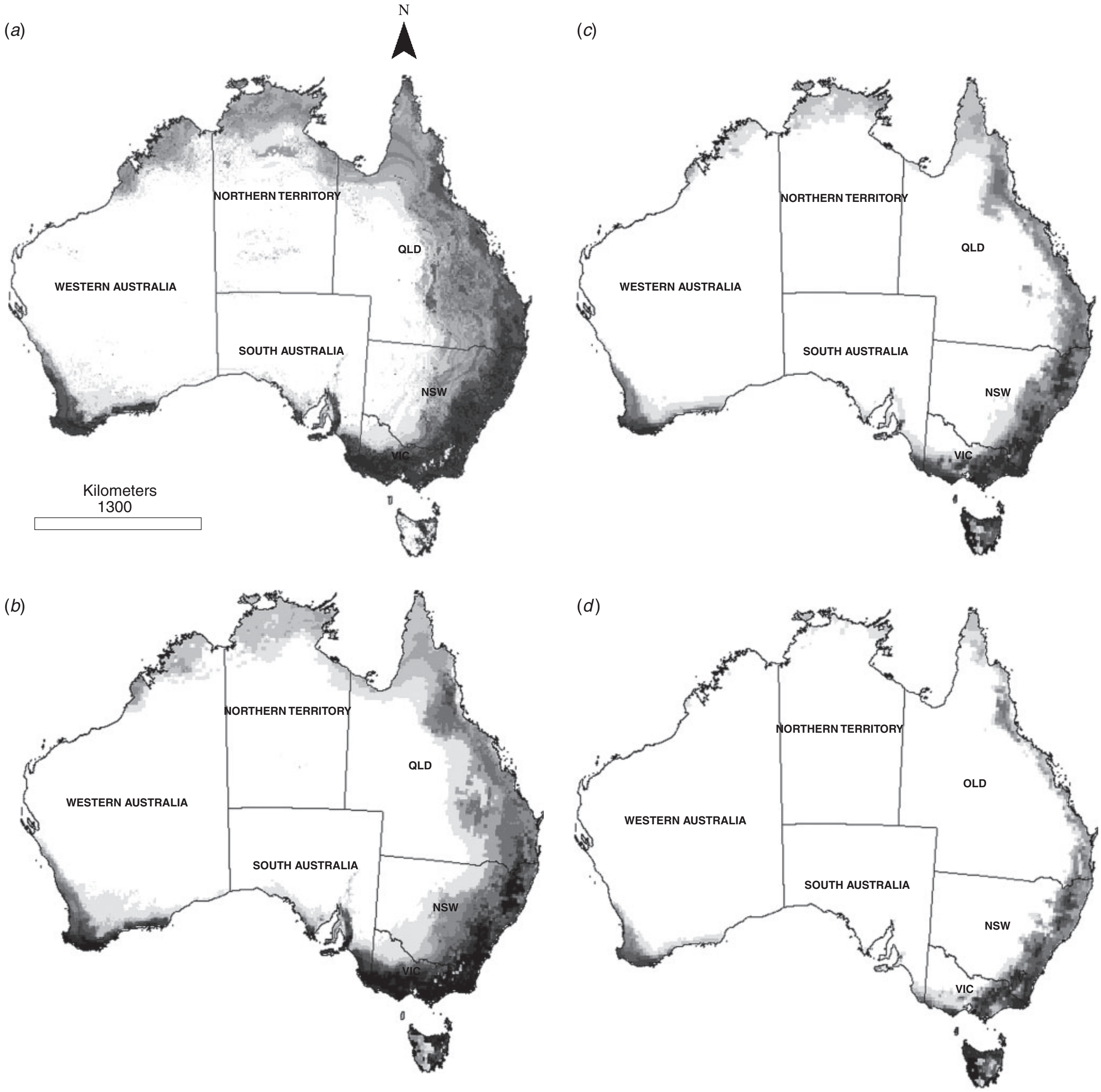

Fig. 2. Maxent predictions for (*a*) current distribution, (*b*) 2030, (*c*) 2050, and (*d*) 2070. Darker shading indicates higher probability of koala occurrence. Source of baseline climate data (1961–90) for current distribution: BOM (2003). Source of A1FI climate change scenarios: CSIRO (2010).

hotter and drier climate in Australia (CSIRO 2007), the koala's climate envelope is predicted to contract eastwards and southwards, with future distributions particularly concentrated in rapidly urbanising regions of coastal QLD and NSW. This represents a dramatic contraction of their current range in the western arid and semi-arid regions of QLD and NSW.

We have identified the current climate envelope of koalas, including novel climatically suitable distributions where koalas do not currently occur naturally. We have also identified the future potential climate envelope of koalas under climate change and in non-analogue climates, i.e. climatic conditions that do not presently exist (Fitzpatrick and Hargrove 2009). The study therefore identifies potentially suitable refuge regions for koalas, which are, or in the future will become, climatically suitable for this species. However, the habitat quality of these climatic refuges is likely to vary locally, and not all identified habitats may be suitable for koalas (e.g. eucalypt forests on coastal ranges or low fertility soils (Crowther *et al*. 2009) or cleared regions). It is important therefore that regional conservation actions aim to protect suitable climate refuge habitats from

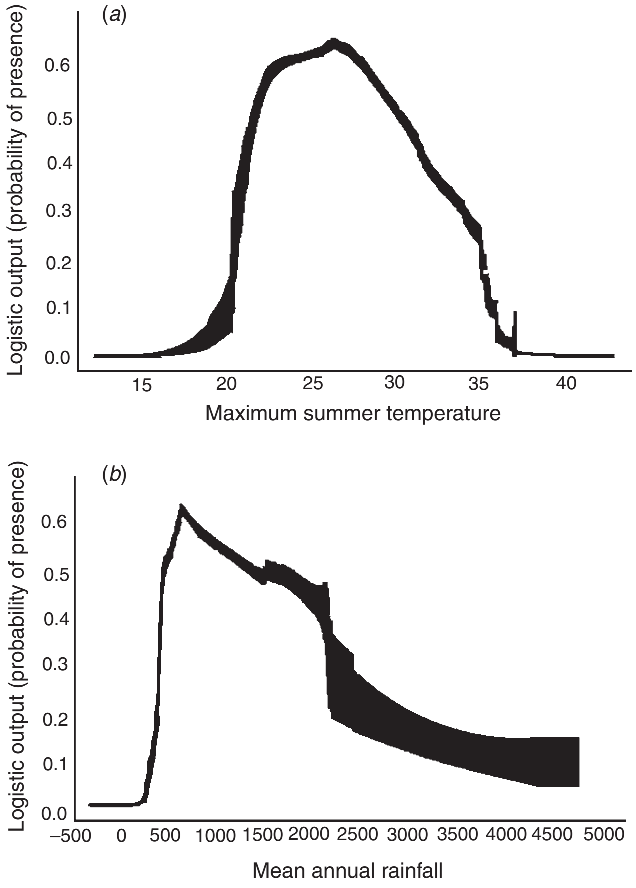

Fig. 3. Mean response curves ±1 s.d. characterising the relationship between koalas and climatic variables (100 bootstrap replicates) for (*a*) maximum summer temperature, and (*b*) average annual rainfall.

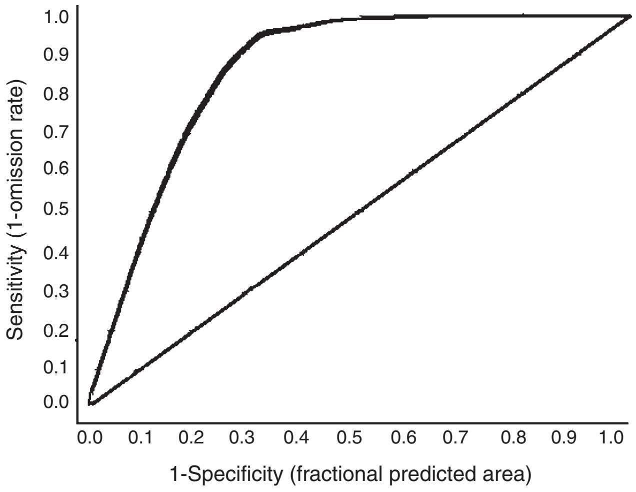

Fig. 4. Model cross-validation showing receiver operating characteristic (ROC) average sensitivity vs 1-specificity (100 bootstrap replicates). Mean receiver operating characteristic curve (AUC) = 0.858. A no better than random AUC is 0.5.

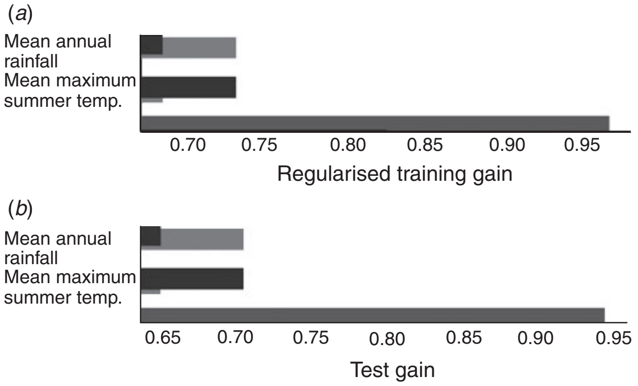

Fig. 5. Jackknife test of variable importance showing mean maximum summer temperature as the most important variable using (*a*) training gain, and (*b*) test gain. Gains are shown in black.

further loss, otherwise the impact of climate change on koalas will be further exacerbated.

The study's identification of potentially suitable climatic environments for koalas outside their current climate envelope is generally consistent with fossil records for koalas in Western Australia (Merrilees 1967; Archer 1972) and far northern QLD (Archer *et al*. 1991; Louys *et al*. 2007). Such records, although highly temporally varied, and including the Lake Eyre region in central Australia (Stirton 1957), suggest that koalas have adapted to past environments and climates over a larger area of the continent, but have contracted to eastern Australia due to climate or vegetation change, or the interaction of both. This highlights the sensitivity of koalas to past climate change and their potential vulnerability to projected rapid climate change.

Climate change and physiological processes

Our preliminary bioclimatic analysis using Bioclim (Nix 1986) indicated that koalas are currently confined to areas with a maximum summer temperature of 37.7°C and maximum annual rainfall of 2480 mm (Table 1). The culmination of ongoing climate-change-induced thermoregulatory pressures on koalas, in particular days that exceed 37.7°C are of serious concern for koalas in many regions of Australia. For example, immediately before the 2009 Victorian bushfires, there were consecutive days over 43°C, with the maximum temperature reaching 46.4°C, and this was preceded by below average rainfall (Victorian Bushfires Royal Commission 2009). At this time, there were numerous anecdotal reports of koalas showing signs of heat and drought stress, for example by drinking from swimming pools in gardens and unable to climb trees. The crash of a koala population following a drought and heatwave in western QLD reinforces these observations (Gordon *et al*. 1988). We have focussed on mean climate, but the predicted changes in extremes such as increased frequency, duration and severity of droughts and heatwaves are likely to exacerbate the effects of changes in mean climate on koalas.

A recent study based on water and energy requirements of another Australian endemic marsupial species with similar dietary requirements, the greater glider (*Petauroides volans*),

Table 1. Bioclimatic profile for *Phascolarctos cinereus* relevant to the Maxent analysis as derived from Bioclim using the koala records applied to the study ($n = 3315$)

Parameter	Mean	Maximum	Minimum
Annual mean temperature (°C)	16.4	24.2	6
Maximum temperature of warmest period (°C)	29	37.7	18.9
Annual precipitation (mm)	863	2480	234

made similar predictions to this study about the impact of a warming scenario (Kearney *et al*. 2010). There are other processes associated with climate change that we have not measured, which are likely to further impact on the future distribution of koalas. For example, the importance of leaf moisture to meet koalas' summer moisture requirements (e.g. Clifton *et al*. 2007), foliar chemistry restrictions (e.g. Moore *et al*. 2004, 2005), and the climatically driven presence of their food sources (Hughes *et al*. 1996) are interrelated factors. Although not investigated in this broad-scale bioclimatic study, it can be expected that there will be parallel contractions in the ranges of both koalas and their food trees under future climate change. The loss of the koala's critical food resources would have major indirect effects on the future distribution of this species under climate change. This would need further investigation at a regional scale.

Approach and limitations

Maxent is a species distribution modelling approach that has been found to perform well under both current climates and future predictions (Hijmans and Graham 2006). It is widely used for modelling shifts in species' distributions (e.g. Fitzpatrick *et al*. 2008; Carroll *et al*. 2010; Kearney *et al*. 2010) and has shown good correspondence with mechanistic models of Australian mammal physiological responses under projected changes in climate (Kearney *et al*. 2010). There are inherent assumptions and limitations associated with any correlative species' distribution or climate envelope model, particularly when considering the complexity of ecosystems. For example, the Maxent modelling approach used in this study does not consider other environmental or anthropogenic factors affecting the distribution of koalas. We recognise that the presence of suitable food trees, especially when occurring on fertile soils, is a critical factor influencing the distribution of koalas (Gordon *et al*. 2006). In addition, models that use the current observed distribution of a species in the context of novel environmental conditions resulting from climate change do not provide information about how the species might respond under novel environments (Fitzpatrick and Hargrove 2009). Issues such as scale mismatch (Wiens *et al*. 2009) and the capacity of a species to adapt, evolve or emigrate must always be considered when using species distribution models to inform conservation planning decisions (Sinclair *et al*. 2010). However, robust species distribution modelling techniques that use presence-only data such as Maxent, which we have used here, provide quantitative guidelines by identifying trends in the distributions of species under future climate change that will assist in the decision-making process. We chose not to calculate the threshold for presence/absence predictions in Maxent, although in some cases it makes sense to create binary maps (Liu *et al*. 2005). However, thresholds are somewhat subjective, and probability predictions in this case provided a more meaningful and truer interpretation of our model, as well as providing some sense of uncertainty.

Conservation and management implications of results

A desired outcome of the National Koala Conservation and Management Strategy 2009–14 (Australian Government 2009) is that the koala remains nationally abundant and widespread, and is not nationally threatened. The impacts on koalas of climate change are recognised in the strategy and our study confirms that western QLD and NSW koala populations are particularly vulnerable to climate change. In effect, koala populations in semiarid and arid regions of eastern Australia will contract their geographic climate envelope with associated declines in population variability unless adequate conservation strategies, such as habitat protection and restoration and conservation incentives to private landholders (e.g. DERM 2010; Fischer *et al*. 2010), are implemented. However, it will be critically important that these efforts are focussed at regional scales, on areas such as those that we have identified as having a high probability of providing future climate refugia.

Another possible conservation management strategy for koalas is assisted colonisation/migration (McLachlan *et al*. 2007; Hoegh-Guldberg *et al*. 2008). This would involve moving koalas outside their current distribution, to future climate refuge regions. For example, the current geographic climate envelope modelled here suggests koalas could survive in the coastal ranges of QLD and NSW, areas of Tasmania and alpine areas of VIC. However, previous koala translocations have been problematic (e.g. Duka and Masters 2005; Cristescu *et al*. 2009) and this strategy would first require extensive prior research to assess the ecological viability and implications of such measures.

This study utilised climate envelope modelling as a proposed decision support tool for koala conservation. We have demonstrated that an important step in the conservation planning process for koalas and other species is identifying areas of current and future climate refugia. Further work at regional and local scales, with refinement of the spatial resolution, is necessary for implementing conservation strategies such as those discussed here. These measures are essential if koalas and other native species are to persist across their natural distributions as landscape modification and climate change progresses.

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