

Species distribution modelling using bioclimatic variables to determine the impacts of a changing climate on the western ringtail possum (*Pseudocheirus occidentalis*; Pseudocheiridae)

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Date submitted: 1 February 2013; Date accepted: 20 June 2013; First published online: 8 October 2013

THEMATIC SECTION
Spatial Simulation Models
in Planning for Resilience

SUMMARY

The ngwayir (western ringtail possum *Pseudocheirus occidentalis*) is an arboreal species endemic to south-western Australia. The range and population of this species have been significantly reduced through multiple anthropogenic impacts. Classified as vulnerable, the ngwayir is highly susceptible to extremes of temperature and reduced water intake. Ngwayir distribution was determined using three different species distribution models using ngwayir presence records related to a set of 19 bioclimatic variables derived from historical climate data, overlaid with 2050 climate change scenarios. MaxEnt was used to identify core habitat and demonstrate how this habitat may be impacted. A supplementary modelling exercise was also conducted to ascertain potential impacts on the tree species that are core habitat for ngwayir. All models predicted a reduction of up to 60% in the range of the ngwayir and its habitat, as a result of global warming towards the south-west of the project area, with a mean potential distribution of 10.3% of the total modelled area of 561 059 km². All three tree species modelled (jarrah, marri and peppermint) were predicted to experience similar contractions in range throughout most of the predicted ngwayir range, although their distributions differed. Populations of ngwayir persisting outside core habitat may indicate potential conservation opportunities.

Keywords: climate change, DIVA-GIS, domain, MaxEnt, Modeco, species distribution models, western ringtail possum

INTRODUCTION

At the regional scale, most species and ecological communities exist within a definable bioclimatic niche, where habitat value is largely controlled by a set of variable climatic parameters including precipitation and temperature (Hutchinson 1957).

When there are changes in these variables, the habitat value for that area will also change (Beaumont *et al.* 2005).

Climate change presents a major threat to biodiversity around the world (IPCC [Intergovernmental Panel on Climate Change] 2007); these impacts are expected to increase in both magnitude and frequency throughout the 21st century (Richardson *et al.* 2011). The task of understanding how species and communities respond to changes in climate is made particularly difficult by the non-linear nature of impacts, which means that not all areas will be affected to the same degree. Climate impacts may vary dramatically between landscapes and in response to a species' or community's sensitivity to that change (Perkins *et al.* 2007; Opdam *et al.* 2009; Yates *et al.* 2010a; Richardson *et al.* 2011).

The Australian continent may be highly vulnerable to global warming impacts (CSIRO & BOM [Commonwealth Scientific and Industrial Research Organization & Bureau of Meteorology] 2007, 2012), with predicted impacts of climate change on Australian biodiversity ranging from mild to severe, depending on the ecology of subject species and communities (Hughes 2003).

South-western Australia (Fig. 1) is recognized as a global biodiversity hotspot (Myers *et al.* 2000). Threats such as land clearing, inappropriate fire regimes, exotic species, pathogens and demands for expanded infrastructure have contributed to a decline in the extent and condition of native vegetation throughout the region (EPA [Environmental Protection Authority] 2007). South-western Australia has been nominated as a region vulnerable to climate change (Klausmeyer & Shaw 2009; Hughes 2011) and has already been affected by global warming in that there has already been a generally significant fall in rainfall, changes in the intensity and frequency of severe weather events and a trend towards increasing mean temperatures across much of this region (Burbidge 2010; Indian Ocean Climate Initiative 2012; Prober *et al.* 2012). Global climate models (GCMs) predict that by the end of the 21st century, in comparison to averages prior to the 1980s, global warming will bring about: a 3–4°C increase in mean temperature, a 30–40% decrease in rainfall, significant changes in seasonality, a rise in sea levels

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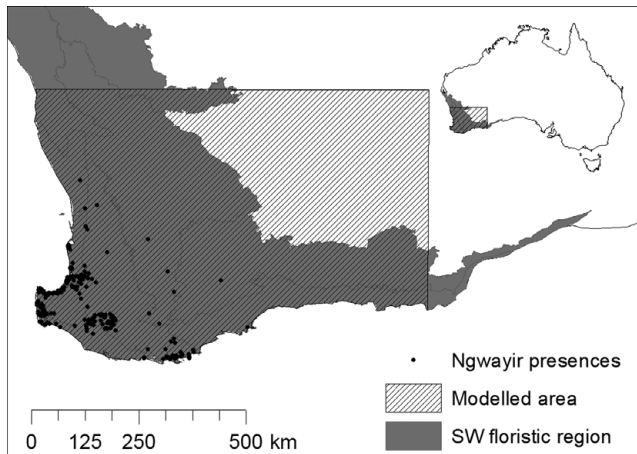


Figure 1 The South-west Australian Floristic Region and sub-regions. Ngwayir presence records and modelled area for this project are overlaid.

and more frequent severe weather events relative to pre-1980s records (CSIRO & BOM 2007, 2012; IPCC 2007; Hughes 2011). Climate variations of this magnitude are likely to have significant detrimental impacts on regional biodiversity (Gritti *et al.* 2006; Cowled 2009; Hughes 2011; Ziska *et al.* 2011; Crossman *et al.* 2012).

Australian protected areas have nevertheless largely been selected without consideration of the impacts of climate change on the reserves themselves or on the needs of species and communities outside of reserves (Dunlop & Brown 2008). Consequently, reserve systems urgently require review to better understand their capacity to withstand the impacts of climate change and to facilitate biodiversity conservation at the landscape scale.

The ngwayir (pronounced 'n-wa-ear') or western ringtail possum (*Pseudocheirus occidentalis*), a small (0.8–1.3kg) arboreal marsupial, endemic to the forests of south-western Australia, provides an ideal candidate to model range shifts in response to the predicted impacts of climate change. This species is listed as vulnerable (Morris *et al.* 2008) and, because of this and its public popularity, is a regional conservation icon (Jones *et al.* 2007; de Tores 2008). The ngwayir is a strict folivore, feeding on a few myrtaceous tree species that meet nearly all of its food and water requirements, and is highly susceptible to extremes of temperature, especially when combined with low moisture levels in leaves (Jones 2004; Yin 2006).

The ngwayir had a pre-European distribution from north of Perth to east of Albany, extending into the Western Australian agricultural region, where populations were recorded in *Casuarina* spp. woodlands until the 1970s (Jones 2004). Local extinction has been extensive in the inland and northern parts of its pre-European range, and the current distribution both patchy and *c.* 10% of the original. The ngwayir now occurs most commonly in coastal or near-coastal forests and woodlands of the southern Swan Coastal Plain, where the

peppermint tree (*Agonis flexuosa*) is a major component of local vegetation (Jones & Howe 1995).

Habitat loss, modification and fragmentation have caused significant negative impacts on ngwayir populations (Wayne *et al.* 2006; Wilson 2009). Much of the coastal area where ngwayir population densities are at their highest is subject to large-scale development pressure from the rapidly-growing human population (EPA 2007; Jones *et al.* 2007; Molloy *et al.* 2007).

The ngwayir is vulnerable to high temperatures and dehydration (Yin 2006), changes in diet, changes in fire regimes (Wayne *et al.* 2006), landscape fragmentation (Jones 2004), feral predators (de Tores *et al.* 2004) and introduced pathogens (Wayne 2009). These vulnerabilities, combined with its rarity, specialized habitat preferences, and low capacity to migrate and disperse, indicate that the ngwayir is likely to be highly sensitive to the predicted impacts of climate change (de Tores 2009). For these reasons, the ngwayir is an ideal candidate to test how effective species distribution models are at determining impacts of anthropogenic global warming on vulnerable species.

Species distribution models (SDMs) are effective in determining current and potential distributions when using climate data alone (Hijmans & Graham 2006; Beaumont *et al.* 2007; Elith *et al.* 2011) allowing historical distributions to be modelled against climate records to form high quality baseline models, which can then be overlaid with GCMs to demonstrate how predicted changes in climate may affect species distributions (Green *et al.* 2008; Yates *et al.* 2010b; Adams-Hosking *et al.* 2011; Fordham *et al.* 2012; Guerin & Lowe 2012; Prober *et al.* 2012). SDMs have become popular in response to increased availability and quality of relevant data (Marcial & Hemminger 2010) and corresponding increases in the availability and complexity of SDMs (Beaumont *et al.* 2005; Guo & Liu 2010).

We investigated potential range shifts of this sedentary, specialist endemic, habitat-restricted vertebrate, in response to the potential impacts of global warming. Our hypothesis is that the ngwayir will be at high risk from climate change. Specifically, we predict that, based on climate change models for south-western Australia, this species will lose much of its core range, and this will further threaten the viability of future populations. We also seek to evaluate the idea that a broader understanding of the impacts of global warming on target species can be obtained by seeking congruence between predictions from multiple spatial distribution models each using multiple climate change scenarios.

METHODS

Model selection

Three SDMs were chosen to examine the impacts of three IPCC IV GCMs on the potential distribution of ngwayir. We used multiple models because our aim was to obtain a broader understanding of the potential impacts of climate change, and

to identify and investigate misleading results arising from anomalies in the application of any one particular model. We selected SDMs that have been shown previously to be successful in predicting species distributions from presence-only data, each employing a different methodology to do so (Guo & Liu 2010; Elith *et al.* 2011). By comparing such diverse SDMs, and applying them to the three most accurate GCMs available, we hoped to gain a more robust understanding of the potential impacts of global warming on this species. We sought congruence between predictions from the different models as evidence for the most likely response of the species to climate change.

We also performed MaxEnt (Phillips *et al.* 2006; Elith *et al.* 2011) analyses on the three tree species most commonly associated with ngwayir habitat: jarrah (*Eucalyptus marginata*), marri (*Corymbia calophylla*) and peppermint (*Agonis flexuosa*). These tree species provide the bulk of the ngwayir's dietary intake and they are keystone species in the ecological assemblages most commonly recognized as ngwayir habitat (Jones *et al.* 1994; Jones 2004; Wayne *et al.* 2005; Yin 2006; de Tores 2008). We conducted tree analyses using the same method and bioclimatic variables as those undertaken for the ngwayir. Because areas identified as being bioclimatically suitable for the ngwayir may not be suitable for the trees upon which it depends, we sought insight into the potential impacts of global warming on ngwayir habitat as distinct from impacts on the animal itself. We present these analyses in the absence of more detailed modelling on the impacts of global warming on the three tree species (Yates *et al.* 2010b; Fordham *et al.* 2012).

We used MaxEnt (Phillips *et al.* 2006) as the principal SDM. Some drawbacks have been noted with MaxEnt, notably the tendency for it to underperform where there is a spatial bias within datasets (see for example Bystrikova *et al.* 2012), however it remains a well-supported and popular application with land managers, and has the capacity to link fine-scale bioclimatic data to species distributions and produce probability-based outputs (Hijmans & Graham 2006; Guo & Liu 2010; Elith *et al.* 2011; Vasconcelos *et al.* 2012). MaxEnt has been successfully used in similar species modelling applications (Green *et al.* 2008; Yates *et al.* 2010b; Adams-Hosking *et al.* 2011; Guerin & Lowe 2012; Prober *et al.* 2012). The two other SDMs we used were Domain (Carpenter *et al.* 1993; Hijmans & Graham 2006) and Two Class Support Vector Machine (SVM-TC) (Vapnik 1995; Cristianini & Scholkopf 2002), both of which generally lack the accuracy and probabilistic capacity of MaxEnt. However, we used these SDMs because the results of the MaxEnt analyses might be further supported and validated by congruence with other models.

MaxEnt (application of a machine learning technique called 'maximum-entropy') explores the relationships between presence data and relevant habitat variables, thereby enabling it to calculate the probability of presence of the target species within a GIS grid square using habitat values (Phillips *et al.* 2006; Hijmans & Graham 2006; Elith *et al.* 2011). MaxEnt

v.3.3.3 for Windows was used in these analyses. Our model settings were 500 maximum iterations with a convergence threshold = 0.00001, prevalence = 0.5 (default) and a 10% training presence. We used a full presence data set for these analyses. Input data were prepared using Diva-GIS 7.5 (Hijmans *et al.* 2012) and output display and analysis for all SDMs were prepared and analysed with ESRI ArcMap 10.1.

SVM-TCs are supervised learning models that analyse data and recognize patterns, which are then used for classification and regression analyses. They take a training sample to build a model used to determine presence or absence in response to variable parameters (Vapnik 1995). SVM-TCs require both presence and absence (or assumed absence) species data. In this study, absence data was not available and assumed absence data was developed at a rate of five absences for every presence using ModEco (Guo & Liu 2010). This was the highest available ratio and was chosen because of the relatively small number of ngwayir presences in the modelled area. SVM-TC was part of the ModEco 3.02 software package (UCMERCED [University of California at Merced] 2011). Our model settings for the SVM-TC analyses were 10% hold out for testing, degree = 3, Nu = 0.05 and cost = 1.

Domain assigns a classification value to an unknown site based on the distance to its closest similar site in environmental space (Carpenter *et al.* 1993) using presence-only data (Tognelli *et al.* 2009; Hawkes 2010; Monk *et al.* 2010; Jimenez-Valverde *et al.* 2011; Khatchikian *et al.* 2011; Navarro-Cerrillo *et al.* 2011). We used Domain in both ModEco and Diva-GIS software packages; the outputs we selected for use in this analysis being those developed using the ModEco software package. Domain outputs can be highly biased by outliers in the presence data, whereas both MaxEnt and SVM-TC have the capacity to recognize and limit the influence of outliers in species presences. Consequently, outliers had to be removed manually when using Domain (Hijmans *et al.* 2012). We produced a separate species database with outliers removed using Diva-GIS and used the resultant 'extract' database in the Domain analyses. Our model settings for the Domain analyses were 10% withheld for testing and 95% similarity threshold.

We only used bioclimatic variables in the predictive modelling because we assumed that global warming is the predominant threat to the ngwayir and that this threat will foreseeably increase in intensity during the first half of the twenty-first century and occur throughout its current and potential distribution. IPCC IV (IPCC 2007) GCMs were downloaded from the International Centre for Tropical Agriculture (CAAFS [Climate Change, Agriculture and Food Security Programme] 2008), and were already downscaled to a 1-km grid spatial resolution using the delta method (Ramirez & Jarvis 2008). We selected the MIROC-m, CSIRO mk3 and ECHO-G models from the IPCC IV group of models, as these three were the most accurate for Australia (Perkins *et al.* 2007). Furthermore, each model represents a different methodology, reflecting the diverse interests, perspectives and objectives of the organizations that developed them (IPCC 2007). The

Table 1 Variable use in SDMs showing the contribution of each variable in the MaxEnt and the variables used in the Domain and SVM-TC SDMs.

<i>Variable</i>	<i>Description</i>	<i>MaxEnt (%)</i>	<i>Domain</i>	<i>SVM-TC</i>
<i>BIO1</i>	Annual mean temperature	5.4		
<i>BIO2</i>	Mean diurnal range (max temp – min temp) (monthly average)	1.1		1
<i>BIO3</i>	Isothermality (BIO1/BIO7) * 100	0.6		1
<i>BIO4</i>	Temperature seasonality (coefficient of variation)	12	1	1
<i>BIO5</i>	Max temperature of warmest period	0.3	1	1
<i>BIO6</i>	Min temperature of coldest period	0.3		
<i>BIO7</i>	Temperature annual range (BIO5–BIO6)	0.3	1	1
<i>BIO8</i>	Mean temperature of wettest quarter	0		
<i>BIO9</i>	Mean temperature of driest quarter	0.3		
<i>BIO10</i>	Mean temperature of warmest quarter	0.6		
<i>BIO11</i>	Mean temperature of coldest quarter	0.9		
<i>BIO12</i>	Annual precipitation	67.1	1	1
<i>BIO13</i>	Precipitation of wettest period	1.1	1	1
<i>BIO14</i>	Precipitation of driest period	1		
<i>BIO15</i>	Precipitation seasonality (coefficient of variation)	3.9		1
<i>BIO16</i>	Precipitation of wettest quarter	1.6	1	1
<i>BIO17</i>	Precipitation of driest quarter	0.1		
<i>BIO18</i>	Precipitation of warmest quarter	0.1		
<i>BIO19</i>	Precipitation of coldest quarter	3.4	1	1

model scenario chosen for all GCMs was the A2A scenario, which was the ‘medium scenario’ for both CO₂ emissions and future energy requirements, on the assumption that extreme predictions might be avoided. Since CO₂ emissions will, most probably, be higher than predicted in this scenario (Allison *et al.* 2009), range contractions indicated in this paper are consequently likely to be conservative in nature. These data were also cut and processed into bioclimatic variables using Diva-GIS, and the same altitude (topographic) data set used to produce the baseline data. All GCMs were based on 2050 scenarios. As GCMs are constantly being reviewed and improved (IPCC 2007), we considered it appropriate that models for post-2050 scenarios be based on more current climate change models as they become available.

We modelled a rectangular section of the South-west Australian Floristic Region (Fig. 1), large enough to encompass all recorded ngwayir occurrences, but not so large as to imbue models with an inflated appearance of accuracy (Elith *et al.* 2011). We considered natural migration of ngwayir beyond this area to be highly improbable given the highly fragmented nature of the Western Australian Wheatbelt (Smith 2008; Lawes & Dodd 2009). Given the highly variable nature of the project area (Hopper & Gioia 2004), we decided that it was appropriate to model data at the highest available resolution (grid cells of 1-km² or 30 seconds) (Hijmans *et al.* 2005).

Data

We obtained presence data for ngwayir, jarrah, marri and peppermint from the Western Australian Department of Environment and Conservation’s NatureMap database

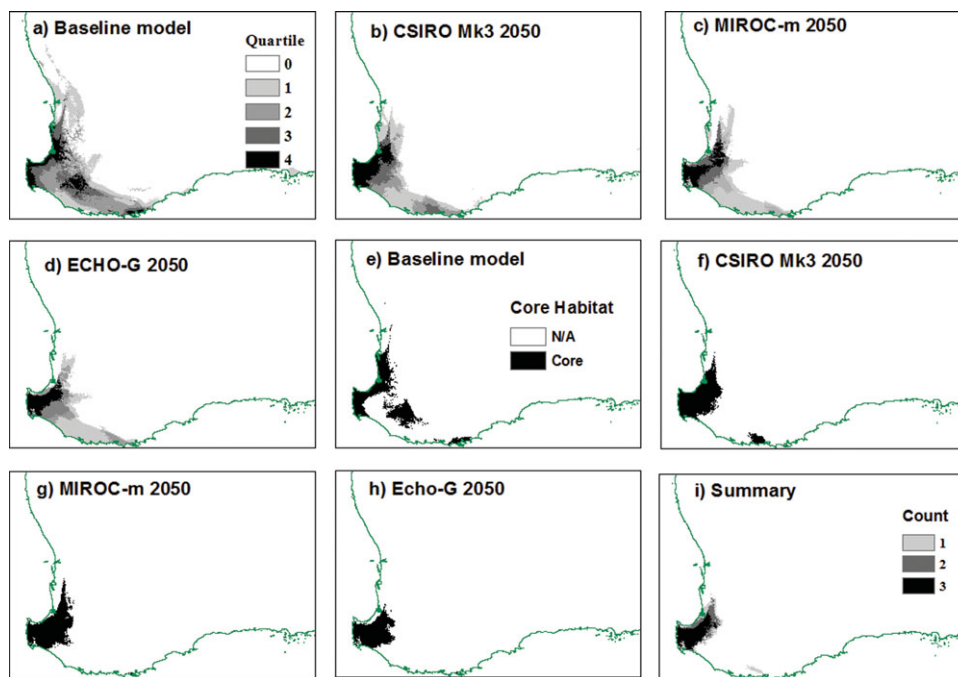
V 1.5.0.10 (DEC [Department of Environment and Conservation] 2007–2013). There were 510 ngwayir presences recorded in this database, which, after disregarding duplicate records and those with erroneous coordinates, resulted in a database of 392 presences. Similarly, 506 presences were used to model jarrah, 344 marri and 374 peppermint; these represent the entire range for each species. These corrected presences were used in both the MaxEnt and SVM-TC analyses. Further correction was undertaken for the Domain analyses. As this data is sourced heavily from extensive surveys across many reserves and remnants, we assumed that sampling bias (such as favouring roadsides or particular regions) was minimal.

Baseline climate data were sourced from the WorldClim 1.4 (release 3) database (WorldClim 2012) of Hijmans *et al.* (2005), developed as interpolated climate surfaces for global land areas other than Antarctica at a 1-km grid cell spatial resolution using 1950–2000 climate data. The WorldClim data were provided in the form of average monthly precipitation, maximum temperature, minimum temperature, mean temperature and topography data that were then cut to the size of the project area and converted into 19 bioclimatic variables (Table 1) using Diva-GIS.

Variable selection

As each SDM uses different algorithms and species inputs, they also require the use of differing sets of variables in their respective analyses (Guo & Liu 2010; Fordham *et al.* 2012). To obtain optimum efficiency, minimize multicollinearity and prevent overfitting (Beaumont *et al.* 2005; Elith *et al.* 2011; Hijmans *et al.* 2012), we first tested the variables

Figure 2 MaxEnt predictions of ngwayir distribution from baseline averages and 2050 GCM scenarios for CSIRO Mk3, MIROC-m and Echo-G IPCC IV models. (a, b, c, d) Modelled probability of presence for each scenario. (e, f, g, h) Core habitat areas derived by applying a cut-off training value, which shows only those bioclimatic values containing 90% of presences. (i) Overlay of core habitat areas. The core area count reflects the number of times each pixel appears as core habitat.



to establish the most appropriate set for inclusion in each SDM analysis. All 19 bioclimatic variables were used in the MaxEnt analyses, as this SDM calculated and implicitly incorporated the percentage contribution of each variable to the final solution (Table 1; Elith *et al.* 2011). Because the contribution of many variables was negligible and tested subsets did not improve on and, in some cases, produced highly unlikely results, we decided that, for the sake of accuracy and consistency, all 19 variables be applied to all MaxEnt models (Phillips & Dudík 2008).

For the SVM-TC and Domain models, the proportionate contribution of variables was not an option. In these situations, variables were either included or rejected based on the results of a kappa analysis, which determined variable contribution. We undertook kappa analyses using Modeco (Appendix 1, Table S1, see supplementary material at Journals.cambridge.org/ENC). For both SDMs, the cut-off for inclusion (Appendix 1, Table S1, see supplementary material at Journals.cambridge.org/ENC) was 0.2, which delivered the best results based on trial and error.

We applied landscape metrics, such as vegetation association, patch size and isolation, in early SDM trials; however these did not improve on the use of bioclimatic variables alone, and modelling results became erratic in a manner symptomatic of overfitting (Welsh *et al.* 2013). Consequently, their use was abandoned.

Core areas were used to display results (maps). We determined core areas by applying the 10% training presence threshold (0.387); only those areas with bioclimatic parameters within which 90% of presences were recorded were designated as habitat. Those areas where we assigned a lesser value were considered marginal habitat, and thus disregarded. This enables conservation managers to focus on those areas that

are likely to more important for the conservation of the target species or community (Phillips *et al.* 2006; Hijmans *et al.* 2012).

RESULTS

The MaxEnt modelling of ngwayir distribution using baseline WorldClim 1950–2000 averages (Hijmans *et al.* 2005) and 2050 model scenarios (for CSIRO Mk3, MIROC-m and Echo-G IPCC IV models; (IPCC 2007) demonstrated a marked and similar contraction of ngwayir distribution towards the south-west, as compared to the total baseline bioclimatic envelope for this species (Fig. 2).

For habitat parameters within which 90% of presences occurred, the contraction in the potential core distribution became much more pronounced for all three GCMs. Potential distribution predictions were remarkably similar for all GCMs, indicating that the modelled GCM scenarios were robust. The area under curve (AUC) goodness of fit value for the MaxEnt model was 0.973, indicating a good model in terms of predictive ability (Phillips *et al.* 2006), further supported by a high 10% training presence value of 0.387.

Each of the SDMs predicted broadly similar baseline patterns of ngwayir distribution and resulted in similar predicted distributions for all three climate change scenarios for 2050 (Appendix 1, Fig. S1, see supplementary material at Journals.cambridge.org/ENC). These predictions show only predicted presences, in that pixels with a probability value of < 5% are not displayed. All models gave a marked and similar contraction in ngwayir potential distribution towards the south-west. Overall, MaxEnt appeared to have a marginally greater sensitivity to topographic variation, selecting low-lying areas in the northern Darling Range and parts of the

Table 2 Areas (km²) selected as habitat for projections (Appendix 1, Figure S1, see supplementary material at Journals.cambridge.org/ENC). Total modelled area = 561 059 km².

<i>Model</i>	<i>MaxEnt area</i>	<i>% Total area</i>	<i>Domain area</i>	<i>% Total area</i>	<i>SVM-TC area</i>	<i>% Total area</i>	<i>Mean area</i>	<i>% Total area</i>
<i>Worldclim (baseline)</i>	59 341	10.58	61 133	10.90	55 106	9.82	58 527	10.43
<i>CSIRO Mk III</i>	44 278	7.89	39 797	7.09	39 007	6.95	41 027	7.31
<i>ECHO-G</i>	35 870	6.39	27 024	4.82	29 948	5.34	30 947	5.52
<i>MIROC-m</i>	44 375	7.91	33 934	6.05	38 780	6.91	39 029	6.96
<i>Mean 2050</i>	41 508	7.40	33 585	5.99	35 912	6.40	37 001	6.59
<i>Mean area reduction</i>	17 833	3.18	27 548	4.91	19 194	3.42	21 526	3.84

lower Blackwood River Basin that were not highlighted in the Domain and SVM-TC models. MaxEnt predicted larger areas of potential distribution (that is, MaxEnt predicted the smallest reduction in core distributions). Domain predicted the greatest reduction in area, although the difference between the mean areas was <2% (Table 2). The AUC and kappa values for both the Domain and SVM-TC analyses indicate that these models are strong (Appendix 1, Table S2, see supplementary material at Journals.cambridge.org/ENC).

The contraction in the potential distribution of ngwayir to the south-west became significantly more severe when the 10% training presence was applied to demonstrate core habitat (Fig. 2e–h). When these projections were overlaid (Fig. 2i), the similarities between them were clear and indicated potentially important landscapes for the conservation of the ngwayir.

Most 2050 projections in this exercise identified highly complementary potential distributions for the ngwayir, with the majority of grid cells identified as potential distribution being the same in all projections. There was a mean baseline area of potential distribution of 10.3% of the total modelled area of 561 059 km², with a maximum area of 10.9% and a minimum of 9.8% (Table 2). All projections showed a significant contraction in area by 2050, to an average 6.6% of total modelled area ranging from a high of 7.8% (MaxEnt/CSIRO) to a low of 4.8% (Domain/ECHO). For all SDMs, the ECHO GCM showed the greatest impact on the ngwayir, with an average 2050 distribution of 5.5%; the MIROC-m and CSIRO models were very similar, with averages of 7.0% and 7.3%, respectively. Of the SDMs, MaxEnt was the most optimistic, with a mean 2050 area of 7.4% compared to an area of 6.4% for SVM-TC and 6.0% for Domain. The similarities between all modelled scenarios, both baseline and predicted, for all three SDMs across all GCMs indicated strongly that the MaxEnt modelling exercise produced a highly plausible scenario.

MaxEnt modelling of the three tree species showed the potential distribution of all three species contracted strongly towards the south-west (Fig. 3). For all species, but particularly for jarrah and marri, there was a tendency for distribution to be split into northern and southern

populations, with the southern populations appearing to be more robust. The CSIRO/Marri projection, and, to a lesser extent, the ECHO/Marri projection, indicated large inland areas becoming suitable for marri; although the reasons for this are not currently understood, these areas were outside the ngwayir dispersal range.

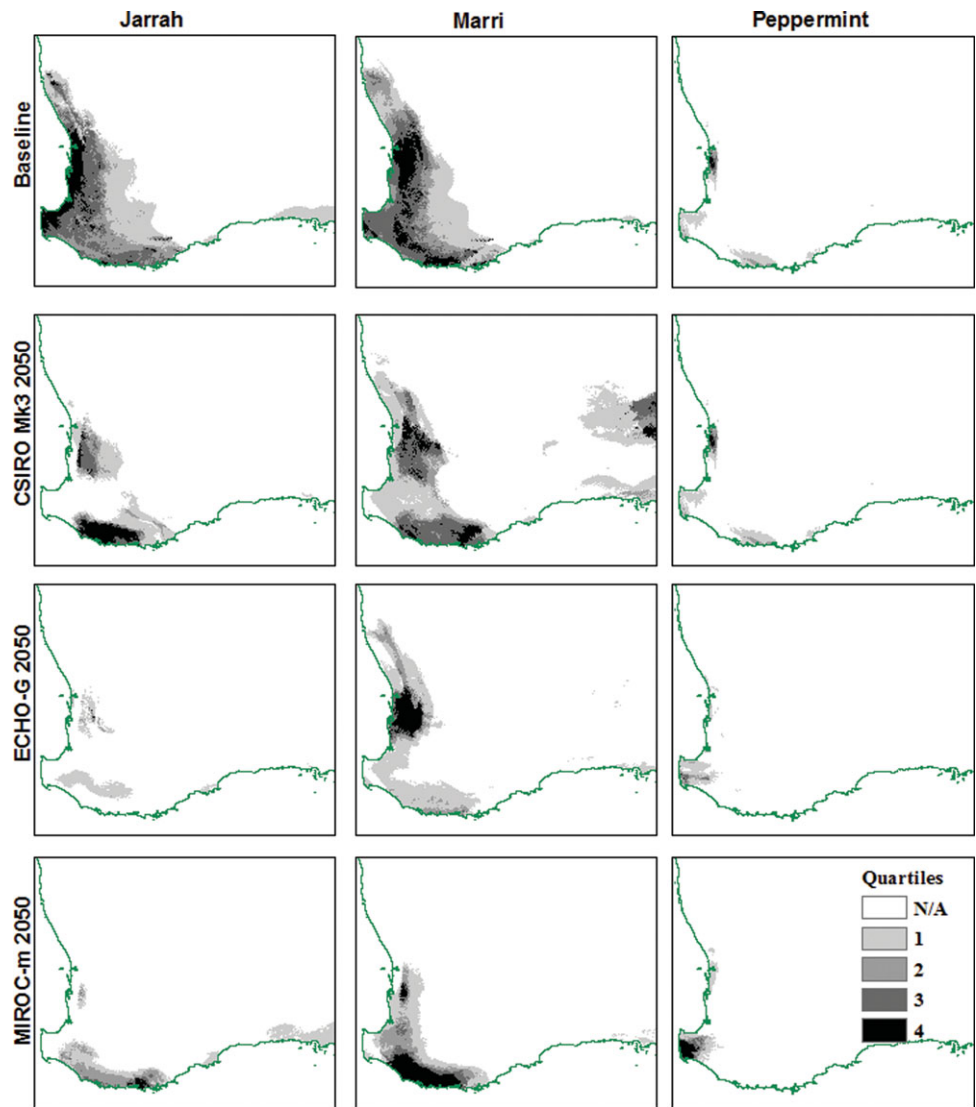
When we compared predicted ngwayir core habitat with that of the three tree species (Fig. 4) and with conservation and forestry land tenure (Appendix 1, Fig. S2, see supplementary material at Journals.cambridge.org/ENC), extensive stands of either jarrah/marri and/or peppermint stands persisted alongside all projected potential model distributions of ngwayir, with much of these vegetation types continuing to occur on conservation/forestry land. It is expected that relictual populations of all of these species will persist beyond 2050, outside of these parameters (Appendix 1, Table S3, see supplementary material at Journals.cambridge.org/ENC). Statistical tests show that all models in these analyses are good, although models for each species differed markedly in the variable contributions used (Appendix 1, Table S4, see supplementary material at Journals.cambridge.org/ENC).

DISCUSSION

In modelling the potential distribution of ngwayir, all three SDMs, although differing in type and sets of predictor variables, predicted similar binary distributions for the species, both for their current distributions and in the projections for 2050. Although there were some differences between the three climate change scenarios for 2050, all nine predictions demonstrated strong support for a significantly reduced ngwayir distribution, with a strong contraction towards the south-west. MaxEnt modelling showed that areas of core habitat within predicted potential distribution areas may suffer greater contractions than the binary outputs indicate. The contraction to the higher rainfall coastal areas of the south-west is consistent with other predictions of species-level climate change impacts within the region (Yates *et al.* 2010a, b).

Although climatic envelope modelling predictions of species contractions due to climate change are now relatively

Figure 3 MaxEnt models comparing baseline distribution of jarrah, marri and peppermint with the three IPCC IV 2050 climate scenarios.



common, it is widely recognized that modellers need to consider habitat preference or quality and potential interactions with other species to more accurately predict future climate change impacts (Williams *et al.* 2008). In this study, we used predicted contractions in the preferred tree species (for feeding and nesting) to further explore potential impacts of climate change on the ngwayir. MaxEnt modelling shows that, although the preferred tree species of ngwayir will also be strongly impacted by climate change, at least one of the core tree species will persist through much of the ngwayir's future predicted distribution. Such severe tree species range contractions are supported by many studies on the observed and predicted impacts of anthropogenic global warming on woodland and forest species throughout the world (Allen *et al.* 2010; Littell *et al.* 2010; Chaturvedi *et al.* 2011; Milad *et al.* 2011; Prober *et al.* 2012). Of the three tree species modelled, the contraction in core peppermint habitat appears to be the most significant and is of most concern, as ngwayir

is most common in the dense vegetation dominated by this species (Jones & Howe 1995; Jones 2004). For two climate change scenarios in particular, core peppermint habitat is predicted to contract to the extreme south-west corner of the landscape. This prediction has important conservation implications, as many reserves with peppermint that currently support healthy populations of ngwayir may not be within the predicted future range of peppermint, highlighting the problems associated with maintaining a static reserve system in the face of climate-induced shifts in species distributions (Williams *et al.* 2008). Although the bioclimatic modelling of the preferred tree species is preliminary, it helps improve understanding of the vulnerability of ngwayir to climate change. In similar fashion, Bateman *et al.* (2012) improved predictions and understandings of climate change impacts on northern bettong in the tropical rainforests of Queensland by combining this with bioclimatic modelling of its major food species.

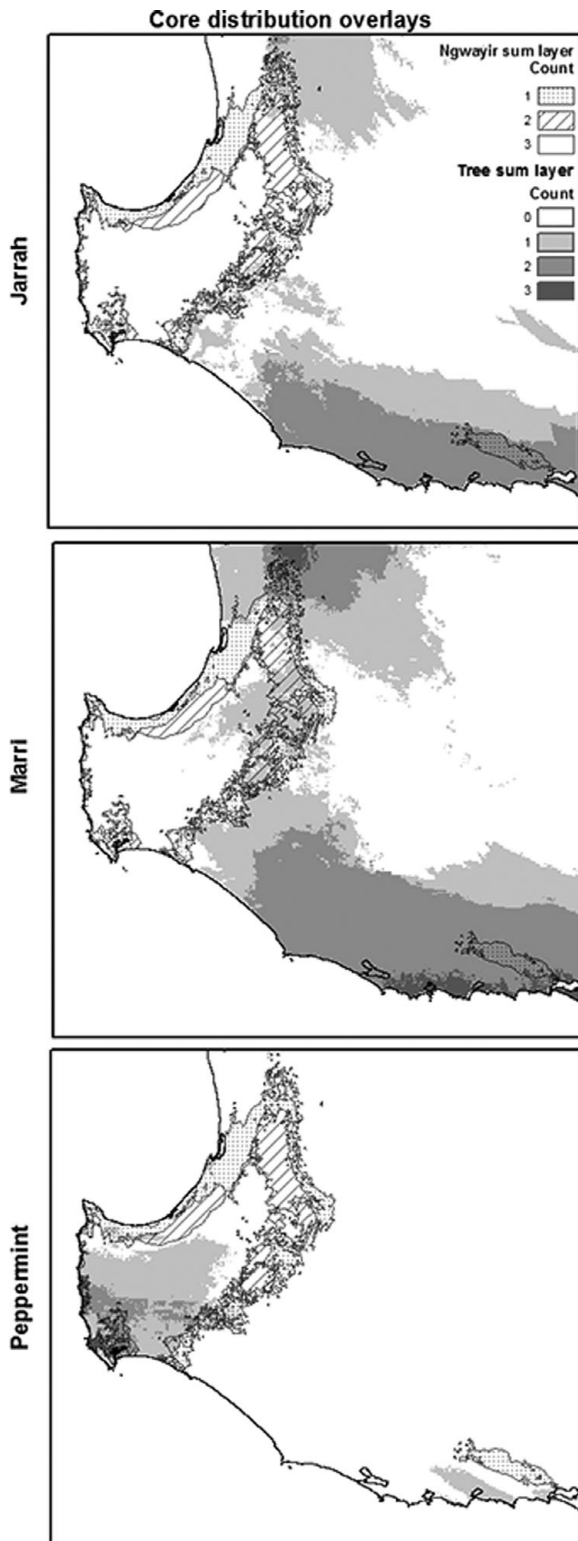


Figure 4 Core area count (the number of times each pixel appears as core habitat) for tree species, overlaid by ngwayir core area count (see Fig. 2).

Unless anthropogenic greenhouse gas emissions decline dramatically, the question becomes one of how to manage a vulnerable species in the face of an almost certain reduction in habitat quantity and quality. This will require further recognition of what landscape parameters actually define habitat for this species at more local scales (Pearson & Dawson 2003; Guisan & Thuiller 2005).

Other factors potentially contributing to the habitat of ngwayir at finer scales, are the feed quality of foliage (which is influenced by the nutrient status of trees) and the quantity and type of volatile oils. As a cecum ruminant, it is probable that ngwayir's habitat choice is influenced by the secondary metabolite content of the plants upon which it feeds (Wallis *et al.* 2002; Moore *et al.* 2004; Scrivener *et al.* 2004; Foley *et al.* 2008). Secondary metabolite levels vary significantly in response to genotypic and phenotypic factors even within plants of the same species, and habitat for many cecum ruminants is often defined by the density of plants, with similarly low levels of secondary metabolites (DeGabriel *et al.* 2008). Areas of suitable foliage can be readily identified through remote sensing techniques, which can also quantify other relevant habitat parameters such as nutrient and moisture levels (Ebbers *et al.* 2002; Malenovský *et al.* 2009). Thus it is possible to remotely identify areas of prime habitat and, by applying bioclimatic modelling techniques, it is possible to obtain a strong indication as to which of these habitats will persist into the foreseeable future. Such areas should be given a high priority for conservation acquisition and management.

It is important to recognize that neither ngwayir movement nor metapopulation requirements have been modelled in this study. This is because no literature defining ngwayir metapopulation requirements exists, and because those areas identified as future potential distribution for the ngwayir are generally contiguous, enabling good landscape permeability. Outside of these contiguous landscapes, there are areas recognized as potential future habitat that are not currently occupied by ngwayir, and to which they cannot naturally migrate. This presents a potential opportunity for ngwayir populations to be established through translocation. However, before doing so, a great many factors would need to be investigated, and any potential translocations should be evaluated on a case-by-case basis using an adaptive management approach (Williams *et al.* 2008).

Our prediction of a significant reduction in the range of the ngwayir and its supporting vegetation as a result of anthropogenic global warming concurs with much research on the adverse impacts of changing climate on forest and woodland ecosystems around the world. The frequency and intensity of such negative effects will increase if greenhouse gas emissions are not reduced (IPCC 2007).

ACKNOWLEDGEMENTS

We thank the Holsworth Foundation for funding this project.

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