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Research

Modelling species responses to extreme weather provides new insights into constraints on range and likely climate change impacts for Australian mammals

Alejandra Morán-Ordóñez, Natalie J. Briscoe and Brendan A. Wintle

A. Morán-Ordóñez (http://orcid.org/0000-0002-5815-6089) (alejandra.moran@ctfc.es), N. J. Briscoe and B. A. White, School of BioSciences, The Univ. of Melbourne, VIC, Australia. AM-O also at: CTFC Centre Tecnològic Forestal de Catalunya, Solsona, Spain.

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Conservation of species under climate change relies on accurate predictions of species ranges under current and future climate conditions. To date, modelling studies have focused primarily on how changes in long-term averaged climate conditions are likely to influence species distributions with much less attention paid to the potential effect of extreme events such as droughts and heatwaves which are expected to increase in frequency over coming decades. In this study we explore the benefits of tailoring predictor variables to the specific physiological constraints of species, or groups of species. We show how utilizing spatial predictors of extreme temperature and water availability (heat-waves and droughts), derived from high-temporal resolution, long-term weather records, provides categorically different predictions about the future (2070) distribution of suitable environments for 188 mammal species across different biomes (from arid zones to tropical environments) covering the whole of continental Australia. Models based on long-term averages-only and extreme conditions-only showed similarly high predictive performance tested by hold-out cross-validation on current data, and yet some predicted dramatically different future geographic ranges for the same species under 2070 climate scenarios. Our results highlight the importance of accounting for extreme conditions/events by identifying areas in the landscape where species may cope with average conditions, but cannot persist under extreme conditions known or predicted to occur there. Our approach provides an important step toward identifying the location of climate change refuges and danger zones that goes beyond the current standard of extrapolating long-term climate averages.

Introduction

There is strong evidence that climate change is already influencing natural systems (Parmesan 2006), and an increasing number of species are projected to be at risk of extinction unless effective mitigation and conservation actions can be implemented (Thomas et al. 2004). Accurate predictions of species responses to projected changes in climate could greatly enhance the effectiveness of conservation actions (Guisan et al.

2013). This need, along with advances in species distribution modelling techniques (SDMs), has led to a proliferation of studies examining changes in species distributions linked to recent climate change (Chen et al. 2011, VanDerWal et al. 2012), as well as predictions of future distributions of taxa across broad geographic scales (Peterson et al. 2002, Thuiller et al. 2005).

To date, modelling studies have focused primarily on how changes in mean temperatures and rainfall are likely to influence species distributions (Porfirio et al. 2014), with less attention paid to the effect of extreme events such as droughts, cyclons and heatwaves, on species persistence. The frequency and severity of extreme weather events such as heatwaves are predicted to increase (IPCC 2014). These extreme conditions can play an important role in regulating population dynamics and thus constrain species distributions (Harrison 2000, Frederiksen et al. 2008, Wernberg et al. 2013), either directly, via thermal stress, or indirectly, by influencing food or habitat availability or disturbance processes such as fire (Andersen et al. 2012, Bateman et al. 2012, Cadenhead et al. 2016). For example, population declines, range contractions and local extinctions of birds and mammals have been reported or predicted in relation to thermal stresses caused by very hot temperatures coupled with drought conditions (Welbergen et al. 2008, McKechnie and Wolf 2010, Krockenberger et al. 2012). In contrast, extreme heavy rainfall events that drive lush vegetation growth are associated with booms of rodent populations in arid and semi-arid zones of Australia and America (Parmesan et al. 2000, Holmgren et al. 2006, Letnic and Dickman 2006, Greenville et al. 2012).

Mechanistic and process-based niche models represent valuable tools that can be used to predict population trends and geographic distributions of species in relation to these direct and indirect impacts of climatic conditions by explicitly accounting for demographic processes and/or physiological tolerances of the target species, as well as daily or yearly variation in weather (Anderson et al. 2009, Kearney and Porter 2009, Briscoe et al. 2016). However process-based models are typically data-hungry, and for most species in most ecosystems in most areas of the world there exists insufficient data, knowledge, expertise and computational resources to fit mechanistic models to a large enough portion of the biota such that they could be widely used for comprehensive conservation planning or ecological impact assessment of climate change (Kearney et al. 2010, Dormann et al. 2012, Peterson et al. 2016). Despite their many shortcomings (Dormann 2007, Jackson et al. 2009, Jarnevich et al. 2015), correlative species distribution models will, for the foreseeable future, remain the most widely used tools to forecast the effects of climate change on biodiversity (Thomas et al. 2004, Thuiller 2007, Franklin 2010, Dormann et al. 2012).

Correlative SDMs relate species' occurrence data to spatial variation in environmental conditions (Franklin 2010). These can be used as a good approximation to process-based models to forecast species distributions under climate change, if the environmental predictors selected for fitting the models are known to directly influence population persistence of the target species (Kearney et al. 2010). While the use of ecologically and biologically meaningful variables in correlative SDMs is widely advocated in the SDM literature (Guisan and Zimmermann 2000, Araújo and Guisan 2006, Elith and Leathwick 2009, Jarnevich et al. 2015), most of the studies forecasting future distribution ranges still rely primarily on the use of long-term average climatic variables (e.g. bioclim variables; Milanovich et al. 2010, Franklin et al. 2013). Recently, biogeographic studies have started to implement predictors accounting for variability and stochasticity of weather for making inferences about current species distribution ranges/patterns (Zimmermann et al. 2009, Reside et al. 2010, Bateman et al. 2012, Seabrook et al. 2014, Briscoe et al. 2016). Studies that have explored the influence of extreme weather conditions on future species distributions (Porfirio et al. 2014, Briscoe et al. 2016) have focused on few species or a small geographic extent, limiting generalization to other species or environments.

Australian mammals present an interesting case study of a group of species that tend to be physiologically constrained by environmental extremes (Kearney et al. 2010, Briscoe et al. 2016). Periodic weather extremes have been identified as constraining the ranges of some Australian mammals (Bateman et al. 2012, Briscoe et al. 2016). Extreme heat can be particularly challenging for large terrestrial endotherms that must minimise heat gained from their environment, while also losing heat produced by their own metabolism (Bartholomew 1966). Across Australia high temperatures are often accompanied by low water availability or high humidity, which can further exacerbate this problem by restricting the use of evaporative cooling – the primary method of heat loss in most mammal species (Adolph 1947, Maloney and Dawson 1998). Because Australia's mammal fauna exists across a wide range of biogeographical regions (from arid zones to tropical environments), there is likely to be some benefit in studying the group as a whole and seeking generalizations about which types of extremes constrain their range. Here we provide the first comprehensive account of how weather extremes constrain the ranges of this diverse group of mammals using a unique spatial dataset compiled for the purpose. We explore the degree to which SDM predictions concur under current and future climate and provide recommendations for modellers seeking robust predictions about species future ranges under changing environmental conditions.

Material and methods

Mammals occurrence data

We accessed presence–only records for all terrestrial mammals from the Atlas of Living Australia (ALA; <http://spatial.ala.org.au/>). Due to incomplete coverage of all Australian states, we also sought data from individual states agencies (see acknowledgments). We filtered and reduced this data set (569 292 records) by: 1) removing gross positional errors on a basis of contemporary knowledge on current and historical species distribution ranges (Van Dyck and Strahan 2008, Churchill 2009, Menkhorst and Knight 2010); 2) retaining only spatially-valid records collected from 1980 to 2013 with maximum point location error of less than 1 km and 3) removing duplicated records: we kept only one observation per species per grid cell (1 km resolution). We modelled only those species with at least 30 records ($n = 197$ species) in order to minimize the possible negative influence of small samples sizes (Hernandez et al. 2006, Wisz et al. 2008). See Supplementary material Appendix 1 for full list of species and information on data availability for each of them.

Model predictors

Interpolated daily and monthly climate data at 0.05° spatial resolution (~ 5 km) were obtained from the Australian Water Availability Project for the period 1977–2012 (Raupach et al. 2009, 2012). Temperature data were corrected with an adiabatic lapse rate of 0.00645°C m^{-1} (Moore 1956, Sturman and Tapper 1996) from the original 0.05° values to a resolution of 0.01° (~ 1 km) based on a digital elevation model (DEM) resampled from its original 0.0025° to 0.01° resolution (GEODATA 9-second DEM ver.3, Geoscience Australia). The spatial resolution of the weather data therefore matched the (approximate) worst case on the spatial point accuracy of the mammals' occurrence data. We used the monthly climate data to create a set of long-term averaged climatic variables representing mean annual trends (e.g. annual rainfall) and seasonality (e.g. annual range in temperature) using the R package 'climates' ver. 0.1.1-3 (VanDerWal et al. 2011). These climate predictors are widely used in species distribution models studies conducted at regional to global scales (Franklin 2010).

From the daily weather data we calculated seven weather variables accounting for extreme conditions that are likely to influence mammal distributions. These included indices describing the magnitude of temperature extremes (5th and 95th percentile temperatures for minimum and maximum daily temperatures, respectively), maximum length of dry spells (maximum run of sequential dry days; rain fall $<$ 1 mm), and rainfall intensity (mean rainfall on days where rainfall $>$ 1 mm). The effects of hot temperatures on mammals are likely to be dependent on water availability and humidity, which influence the use and effectiveness of evaporative cooling (Adolph 1947, Maloney and Dawson 1998, Krockenberger et al. 2012). Therefore, we also calculated mean vapour pressure during hot weather, the maximum length of heatwaves, as well as the sum of temperatures during the longest run of sequential dry days (rainfall $<$ 1 mm) (Table 1). All weather and climatic predictors were mapped at 1km grid cell resolution. Models were only based on a subset of the above mentioned variables with maximum Pearson's pairwise correlation of 0.7 (Tabachnick and Fidell 1996, Dormann et al. 2013) (see Table 1 for a description of the retained variables and Supplementary material Appendix 2 for a full list of the variables considered for the analyses and correlation matrices). These correlations were calculated across all mammals' occurrence records of the filtered data set (background points), and assessed for each of the predictor sets individually and jointly.

Some remote areas in central and western Australia had sparse rainfall data (Supplementary material Appendix 3) and therefore, interpolation of data in these areas might be insufficient to meaningfully define rainfall patterns in these areas, affecting the calculation of many of the climatic and weather extremes variables explained above. We ran preliminary analyses to identify the boundaries of these sparsely-gauged parts of the continent and to assess the effects of their inclusion into modelling outputs. Areas with sparse station data were masked out of further analysis in order to minimize the effect of these interpolation errors in our subsequent analyses (Supplementary material Appendix 3).

In addition to weather variables, a remotely sensed average vegetation height variable was included in all predictors sets (AVG, EXT and COMP) to capture some of the variation relating to underlying habitat type and site productivity

Table 1. Environmental predictors retained for modelling. A check mark denotes the predictors included in each of the predictors sets used to fit the species distribution models: the long-term mean climatic variables only (AVG model; five predictors); the extreme weather variables only (EXT model; five predictors) and all extreme weather variables plus the long-term averaged annual precipitation (COMP; six predictors).

Variable name	Description	Resolution	AVG	EXT	COMP
Climate: averages					
Bio1	Annual mean temperature	0.05°	✓		
Bio3	Isothermality: mean diurnal range /annual temperature range	0.05°	✓		
Bio4	Temperature seasonality (standard deviation)	0.05°	✓		
Bio12	Total annual precipitation	0.05°	✓		✓
Weather: extremes					
T5	5th percentile of minimum temperature (across all years)	0.05°		✓	✓
av.vpr.hot	Average vapour pressure on days when maximum temperature exceeds T90 (maximum temperature $>$90th percentile)	0.05°		✓	✓
av.sum.temp	Sum of maximum temperatures during maximum run of dry days (rainfall $<$1mm), (average across years)	0.05°		✓	✓
av.m0v.hot	Maximum run of hot, dry days (maximum temp $>$T90, rainfall $<$1mm) (average across years)	0.05°		✓	✓
Vegetation structure					
veg.hgt	Forest canopy height (Simard, M. et al. 2011)	1 km	✓	✓	✓

(Simard et al. 2011) (Table 1). We chose not to include coarse categorical variables relating to vegetation composition (land cover classes -e.g. National Vegetation Information System of Australia; ESCAVI 2003) due to constraints on the number of observation data points for several species and concerns about over-fitting with categorical variables using numerous degrees of freedom. Note that the vegetation height variable is assumed constant in future predictions due to the lack of information about future distribution of vegetation type and structure, growth, and disturbance.

Modelling framework

We modelled the distribution of mammal species using MaxEnt (ver. 3.3.3k; Phillips et al. 2006, Phillips and Dudík 2008), a machine learning method designed for dealing with presence–only data (Elith et al. 2006, 2011) while taking into account the distribution of environmental predictors in the background area of analysis. For each species we fitted three sets of Maxent models using the average vegetation height predictor plus: 1) the long-term mean climatic variables only (AVG model); 2) the extreme weather variables only (EXT model) and 3) all extreme weather variables plus the long-term averaged annual precipitation (COMP) (see Table 1 for the detailed list of predictors included in each of these predictors sets). This allowed us to test for differences in model predictive performance and spatial predictions of habitat suitability based on long-term mean climatic variables versus extreme weather variables, as well as the effect of using both predictor types in the same model (although, because all temperature related variables were strongly correlated, the only long-term mean climatic variable that could be included in the COMP model was annual precipitation).

Exploratory analyses showed that species records were biased towards areas of high accessibility (e.g. roads and urban areas). Biased survey data can lead to environmentally and geographic biased predictions that might reflect the sampling effort rather than the species' true distributions across the study area (Phillips et al. 2009, Kramer-Schadt et al. 2013, Syfert et al. 2013, Lahoz-Monfort et al. 2014). In order to reduce the possible effect of geographical bias in presence data on SDM predictive performance, we provided background points to MaxEnt in such a way as to copy the geographic and environmental bias of the occurrence records (sensu Phillips et al. 2009; Syfert et al. 2013) by using as background all available records for mammals (76 980 records after removing duplicate records per grid cell). This approach, known as the 'target-group background' approach (Phillips et al. 2009), has been shown to perform well in dealing with spatial sampling bias (Syfert et al. 2013, Fithian et al. 2015). The same background points were used in all three sets of models.

In addition to controlling the selection of background points, we also controlled the complexity of the response shapes by allowing only linear, quadratic and product features in the models. These are similar to linear, quadratic and interaction terms in regression models. Models with these restricted feature types will be smoother than those fitted with MaxEnt's default settings, less prone to fitting idiosyncrasies of the data, and potentially better at predicting to new times and places (Merow et al. 2014). Default values were used for all other MaxEnt settings except that adding sample points to the background was not required as that was already achieved by our use of the 'target background' approach. Predictive performance was assessed in terms of discrimination ability measured using the area under the receiver–operator characteristic curve (AUC; Hanley and McNeil 1982) adapted for use with presence–background samples (Phillips et al. 2006). This metric is suited to presence–background data, since calibration cannot be assessed and applying thresholds to predictions loses information (Guillera-Arroita et al. 2015, Morán-Ordóñez et al. 2016). We calculated AUC using the ten-fold cross-validation provided in Maxent. Final reported models were also run using 100% of the data available for each species. We refer to the later as 'alldata' models and they were only used to compare future predictions based on the different data sets (AVG, EXT and COMP).

Integration of model results across all species

We used boxplots to analyse the differences in predictive performance (cross-validated AUC) of the three sets of models across all species ($n = 197$). To examine spatial differences in predictions, we calculated the differences in the relative environmental suitability values predicted across the landscape between the three model data sets: '$\text{alldata}_{\text{EXT}} - \text{alldata}_{\text{AVG}}$', '$\text{alldata}_{\text{COMP}} - \text{alldata}_{\text{EXT}}$' and '$\text{alldata}_{\text{COMP}} - \text{alldata}_{\text{AVG}}$'. For these analyses, we omitted species for which models performed poorly based on at least one of the three model data sets (cross-validated $\text{AUC} < 0.7$; Swets 1988) as these can not reliably characterise the current distribution of the species ($n = 188$). These comparisons were based on the models fitted with all of the available observation data (i.e. not the cross-validation subsets). This allowed us to identify the areas across the continent where one predictor set predicted higher or lower relative environmental suitability for a given species in comparison with the other model data sets. The difference maps for each species were aggregated across species; providing the mode of the differences across the 188 species for each pair of predictor variable data types (e.g. EXT vs AVG) at each grid cell. This addresses the question of whether the relative suitability of the cell is predicted to decrease or increase at each grid cell for most of the species when fitting the models using EXT predictors compared with AVG predictors. The output of these joint analyses is a binary map showing the areas where the use of one predictor set (e.g. EXT) increases or reduces relative environmental suitability predictions compared with other predictor variable types (e.g. AVG). To explore which variables could be driving the differences in predictions between the two model sets we analysed the distribution of the values of the original predictors in those areas (Table 1).

Future scenarios

To illustrate how the use of different climate variables (EXT, AVG) could influence forecasts of species' responses to climate change, we also predicted mammal distributions for the year 2070. Acknowledging the potential importance of GCM variability in analysing the impacts of climate change on biodiversity (Diniz-Filho et al. 2009, Synes and Osborne 2011, Harris et al. 2014) we compared forecasts of species' responses under two general circulation models (GCM), the ACCESS 1.3 (CSIRO: Bi et al. 2013) and the CanESM2 (Canadian earth system model; Chylek et al. 2011) and the emissions scenario RCP8.5 (Riahi et al. 2011). We modelled future climates under RCP 8.5, a high emissions business as usual scenario, because observed emission trends appear to be tracking these projections (Peters et al. 2013).

Relative to other possible futures, the ACCESS 1.3 scenario modelled here represents a relatively hot and dry climate future for Australia, with CanESM2 predicting more variable changes in rainfall across the continent. Downscaled projected monthly changes in temperature, humidity, and rainfall for 2070 were obtained as the differences from the base period (1990–2009) using SimClim (1 km resolution; Yin et al. 2013) and assuming greenhouse gas concentrations for RCP8.5 and a moderate response to increased CO_2 concentrations (Riahi et al. 2011). We then used the offset (or change factor) method to construct future daily weather data by combining the change signal from these GCM outputs with observed weather datasets (CSIRO and Bureau of Meteorology 2015), an approach previously used in impact assessments (Cullen et al. 2009, Bell et al. 2012). At each site we splined predicted monthly changes in temperature and humidity to predict daily changes over an annual cycle, with these then added to daily weather data for 1990–2009. 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. Changes in the temporal pattern of 'rainy days' were therefore driven by changes in rainfall that resulted in days that were previously classified as 'rainy days' being classified as 'dry days' (i.e. if rainfall fells below 1 mm) and vice versa. While climate change may also alter rainfall patterns, for example by increasing the frequency of heavy rainfall events followed by longer dry spells, spatial and temporal predictions of how changes in variance are likely to influence patterns of daily weather and extremes across all of Australia were not available at the time of our study. Future climate average and extreme weather variables were then calculated from these derived daily future weather data.

Long-term averaged and short-term extreme weather variables were used to generate predictions of mammal distributions for 2070 using the three sets of MaxEnt models fitted under the current climate (AVG model, EXT model and COMP). We compared the spatial predictions of AVG, EXT and COMP model projections for the current and 2070 climates and measured the correlations between their spatial outputs, and the extent of predicted temporal change in suitable ranges (calculated as the sum of cell values of the logistic MaxEnt output across Australia). We used the limiting factors tool of MaxEnt (Elith et al. 2010) to explore which variables limit the predicted geographic distribution of mammals the most both currently and under the 2070 climatic/weather scenarios. This tool identifies the variable X that could increase environmental suitability the most at a given grid cell when its actual value is changed by its mean value across the training data. We also used the MESS map tool of MaxEnt (Multivariate Environmental Similarity Surface; Elith et al. 2010) to assess the proportion of novel environmental space in each model prediction, under both current and future scenarios (i.e. the level of environmental extrapolation). We calculated the percentage of grid cells across Australia with values outside the environmental ranges captured by the target-group background data used to fit the models. All statistical analyses were performed in R (R Core Team).

We also explored whether the differences in spatial predictions of AVG, EXT and COMP model projections for current and 2070 climates were related to species traits. We collated available trait data for the mammal species modelled (body mass, activity cycle and geographic breath) and plotted the relationship between these traits and the aspects of model prediction evaluated here (correlations between spatial output predictions and differences in predicted ranges). In addition, we assessed whether differences in range projections varied between species occupying different primary climatic zone/s.

Results

There was a relatively high correlation between predictions, and high congruence in predictive discrimination between modelling approaches based on average, extreme and composite climate variables. However, the relatively high correlation between predictions broke down when predicting to future climates due to the divergence in spatial patterns of average and extreme climate predictors.

Current distributions

The predictive discrimination of models tested using cross-validation did not differ markedly between the three sets of climatic/weather scenarios (AVG, EXT and COMP), with moderate to high predictive performance across most species ($AUC \geq 0.7$; Fig. 1). Only 9 out of 197 mammal species showed poor predictive performance across at least one scenario ($AUC < 0.7$; Supplementary material Appendix 1). These nine species had low predictive performance across all three variable sets, and were not considered for subsequent analyses.

For many species predictions of environmental suitability differed spatially between models that utilized different

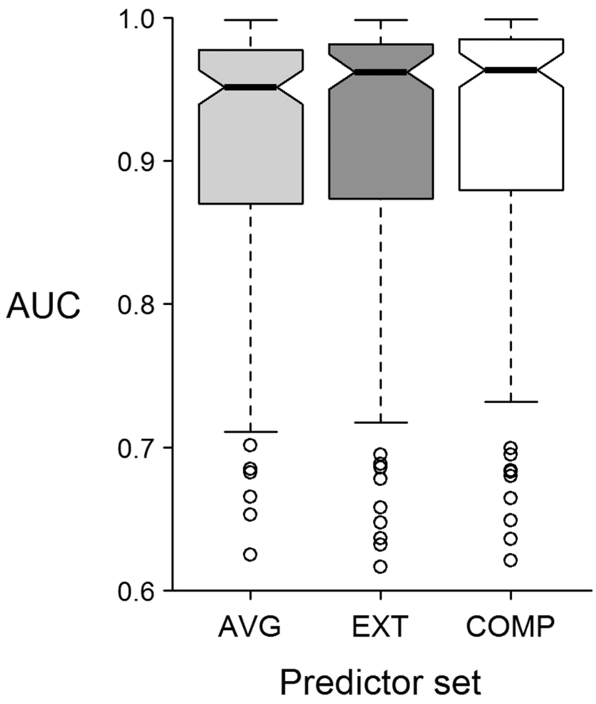

Figure 1. Notched boxplots for AUC values (area under the curve statistic) for all cross-validated mammals' models (n = 197 species), detailed for climate/weather predictor-set: AVG (models using long-term averaged climatic conditions), EXT (averaged short-term extreme weather conditions) and COMP (averaged short-term extreme weather conditions plus long-term average annual rainfall). In each boxplot, the boxes delimit interquartile ranges (25th and 75th percentiles), the whiskers delimit ~2 standard deviations. The notches are centred around the AUC median values (horizontal bolded line) and the outliers are represented as open circles. The lack of overlap between the notch – narrowing around the median – of two boxes offers evidence of a statistically significant difference between the medians. Note that the Y-axis is truncated to the range of observed AUC values (0.6–1).

predictor variables. Models fit using averaged short-term extreme weather predictors (EXT) predicted higher environmental suitability compared to models fit using long-term averaged climatic predictors (AVG) for most species across Tasmania, the southeast and southwest parts of continental Australia, as well as some small areas in the northeast coast of Australia (Fig. 2a, b). Areas where higher environmental suitability was predicted by the extremes models for the largest number of species (areas with darker colours in Fig. 2a), are characterized by either their low average annual mean temperature (< 10°C; Fig. 2c), very low – < 5th percentile – minimum temperatures (< –5°C; Fig. 2g), high rainfall (> 2000 mm; Fig. 2f), high vegetation height (> 40 m; Fig. 2k) and/or for being areas where the contrast between the diurnal temperature range differs markedly from the annual temperature (isothermality values < 0.4; Fig. 2d). The areas where lower environmental suitability was predicted for the largest number of species when using extreme weather predictors instead of long-term average climatic predictors (areas with lighter colours in Fig. 2a and grey areas in Fig. 2b) were characterized by one or more of the following conditions: high average annual mean temperatures (≥ 25°C; Fig. 2c); high 5th percentile minimum temperatures (≥ 10°C, tropical and subtropical regions; Fig. 2g); areas where there is either very high humidity or very low humidity during hot weather (tropical and arid zones, respectively; Fig. 2h); areas that experience very high temperatures over long dry spells (areas in the central and northwest of Australia; Fig. 2i, j); and areas with low seasonality (Fig. 2e) where the diurnal temperature range does not differ much from the annual temperature range (mainly the tropical regions of the north of Australia; Fig. 2d).

Models fit on short-term extreme weather conditions plus annual rainfall (COMP) showed very similar spatial patterns to models fit on extreme weather conditions only (EXT). Therefore, the comparison between COMP and AVG models yields near identical results to the comparison between EXT and AVG models (Supplementary material Appendix 4, Fig. A4.1). However, COMP models predicted a decrease in environmental suitability compared to EXT models for most species in areas with high annual rainfall (mainly the western coast of Tasmania and the northeast coastal areas of continental Australia) and an increase in environmental suitability in the northwest of Australia (Supplementary material Appendix 4, Fig. 4.2).

Current vs future distribution predictions

We found that the relationship between averages and extreme weather variable models were very similar under both GCM scenarios (Supplementary material Appendix 5). Thus, for simplicity, and because we are interested in exploring the variation in predictions due to the variables set selection rather than the variation associated to different GCM scenarios, we focus here on the results from simulations using one scenario only (ACCESS 1.3).

In general, Pearson's correlations between environmental suitability maps of AVG, EXT and COMP models were lower under the 2070 hot and dry climate scenario than under current climate/weather, suggesting a divergence in predictions of environmental suitability under future climate change (Fig. 3a, 4). These results were consistent even when assessed only within the extent of the biogeographical regions where the species is known to occur currently (Supplementary material Appendix 6). For most of the species the decrease in correlations between current and 2070 climate scenarios was less than |0.2| across all predictor sets (Fig 3b). However, for 13 of the 188 species modelled, Pearson's correlations between environmental suitability maps dropped from r > 0.6 (highly correlated) to r < 0.36 (weakly correlated) under the 2070 climate scenario when comparing EXT vs AVG models, and for 19 species when comparing COMP vs AVG models (Fig. 3a, b).

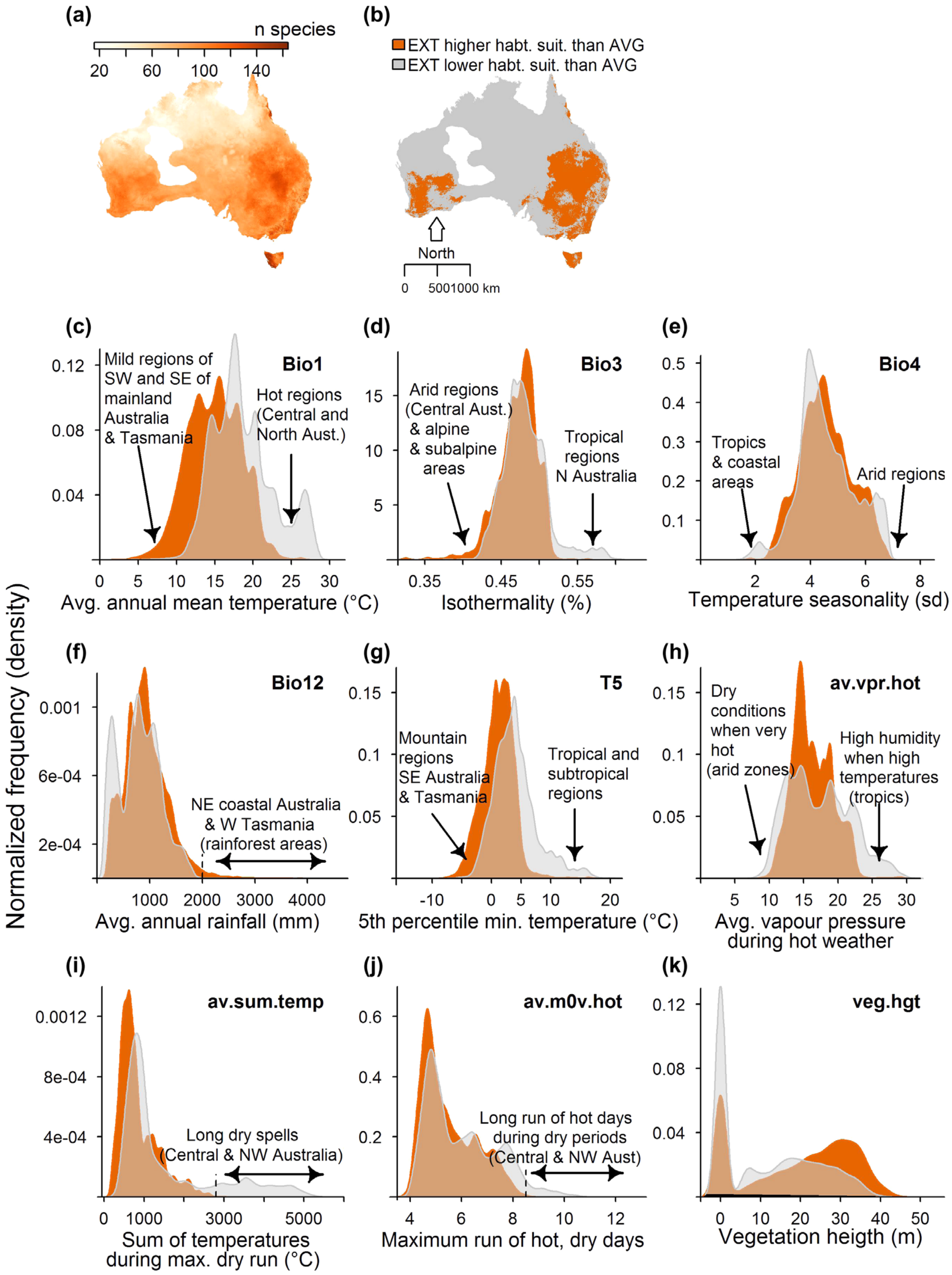

Figure 2. (a) Spatial variation in the number of species for which models fit using short-term extreme weather conditions (EXT) predicted higher habitat suitability than models fit using long-term averaged climatic conditions (AVG); (b) Difference between spatial predictions of EXT and AVG models. Areas of the continent where EXT models predict higher environmental suitability than AVG models for most of the species are shown in orange, with regions where EXT models predict lower environmental suitability than AVG models for most species shown in grey; (c–k) Density plots for the predictors used to fit EXT and/or AVG models (see Table 1 for a full description of these predictors). These plots (c–k) show the range of values of each predictor in each one of the two zones defined in Fig. 2b, and the frequency at which those values occur across the landscape: the orange curve shows the distribution of the predictors' values in the areas where EXT models predict higher environmental suitability compared to AVG models for most of the species; the grey curve shows the distribution of predictors' values in the areas where EXT models predict lower environmental suitability compared to AVG models for most of the species. Arrows point to areas of the environmental space where the values of predictors contribute to explain the differences in spatial predictions of EXT and AVG models.

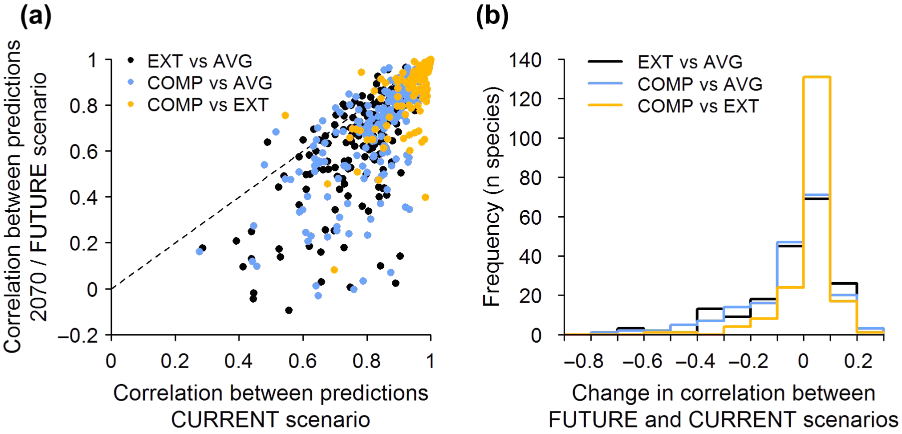

Figure 3. (a) Pearson's correlations between the environmental suitability maps of models fit on the three predictor-sets (AVG, EXT and COMP), under current climatic/weather conditions (current scenario – x-axis) and under a hot and dry climate future scenario for 2070 (2070 scenario – y-axis); points aligned to the dashed black line indicate species for which the correlation between environmental suitability maps was constant over current and 2070 climatic scenarios; (b) Range of changes in Pearson's correlations of environmental suitability maps between 2070 and current climates (x-axis) for each pair of predictor sets (EXT vs AVG, COMP vs AVG and COMP vs EXT). The y-axis indicates the frequency (number of species) at which those changes in correlation were observed across the data (n = 188 mammal species). Composite (COMP) and extreme-only model predictions for 2070 are, on average, more highly correlated than composite and long-term-average predictions, reflecting that extremes variables are contributing more to composite models than the long-term-average variables.

Across the 13 species that showed large declines in correlations between current future scenarios, future divergences were most commonly due to the fact that the EXT and COMP models predicted large changes in distribution relative to the AVG model predictions (Supplementary material Appendix 7). For example, environmental suitability predictions for the paucident planigale *Planigale gilesi* were similar between AVG, EXT and COMP models under current climate (all models identified the central parts of the continent as the most suitable for this species) (Fig. 4). In contrast, whereas the AVG model predicted that areas predicted to be suitable for the planigale under the current climate would remain suitable under the 2070 climatic scenario, EXT and COMP models predicted dramatic shifts in the distribution range of the species in slightly different directions (from central Australia towards the south and southeast coast; Fig. 4). For this species, the shifts in the suitable conditions predicted by EXT and COMP models seem to be driven by the increase in the length of heatwaves (*av.m0v.hot*) predicted under the 2070 scenario (Fig. 4). In some other cases, the change in predictions' correlations over future scenarios arises because one of the predictor-set models predicted limited or zero environmental suitability for a species under 2070 scenario whereas other models predicted the maintenance of the suitable environmental range over time or even an increase in environmental suitability (see further examples in Supplementary material Appendix 7).

In general terms, under the 'current' climate scenario the extent of suitability predicted by EXT and COMP models tended to be smaller than those predicted by AVG models, although this difference was not evident when we included only biogeographical regions where the species is known to occur currently (Fig. 5, Supplementary material Appendix 6, Fig. A6 d, f). Under the 'current' climate COMP models predicted slightly more restricted suitable distribution ranges than EXT models (Fig 5). Under the future climate scenario, differences in the extent of predicted suitable range showed a high variability across species and predictors sets.

The amount of extrapolation to novel environments (as measured by MESS maps) was larger in EXT and COMP models than in AVG models under both current and – especially – future climate scenarios. Under the current climate, novel climatic conditions were found in 0.08, 0.11 and 0.12% of the total study area for AVG, EXT and COMP predictions, respectively. These percentages increased to 20.6, 57.8 and 59.9%, respectively under the future climatic scenario. The areas of non-analogue climate under the future scenario are located mainly in the central and northern parts of the continent (Supplementary material Appendix 8).

We found no clear evidence for an effect of species traits on the magnitude of divergence of predictions between AVG, EXT and COMP models (Supplementary material Appendix 9). The reduction in suitable range predicted by EXT models compared to AVG model under future climate scenario was marginally larger for species that occupy – totally or partially – desert areas or areas of hot and dry summers and mild winters (Supplementary material Appendix 9, Fig. 9.1) than for species characteristic of other climate zones.

Discussion

Conservation of species under climate change relies on accurate predictions of both the extent and suitability of species ranges under current and future climate conditions. We

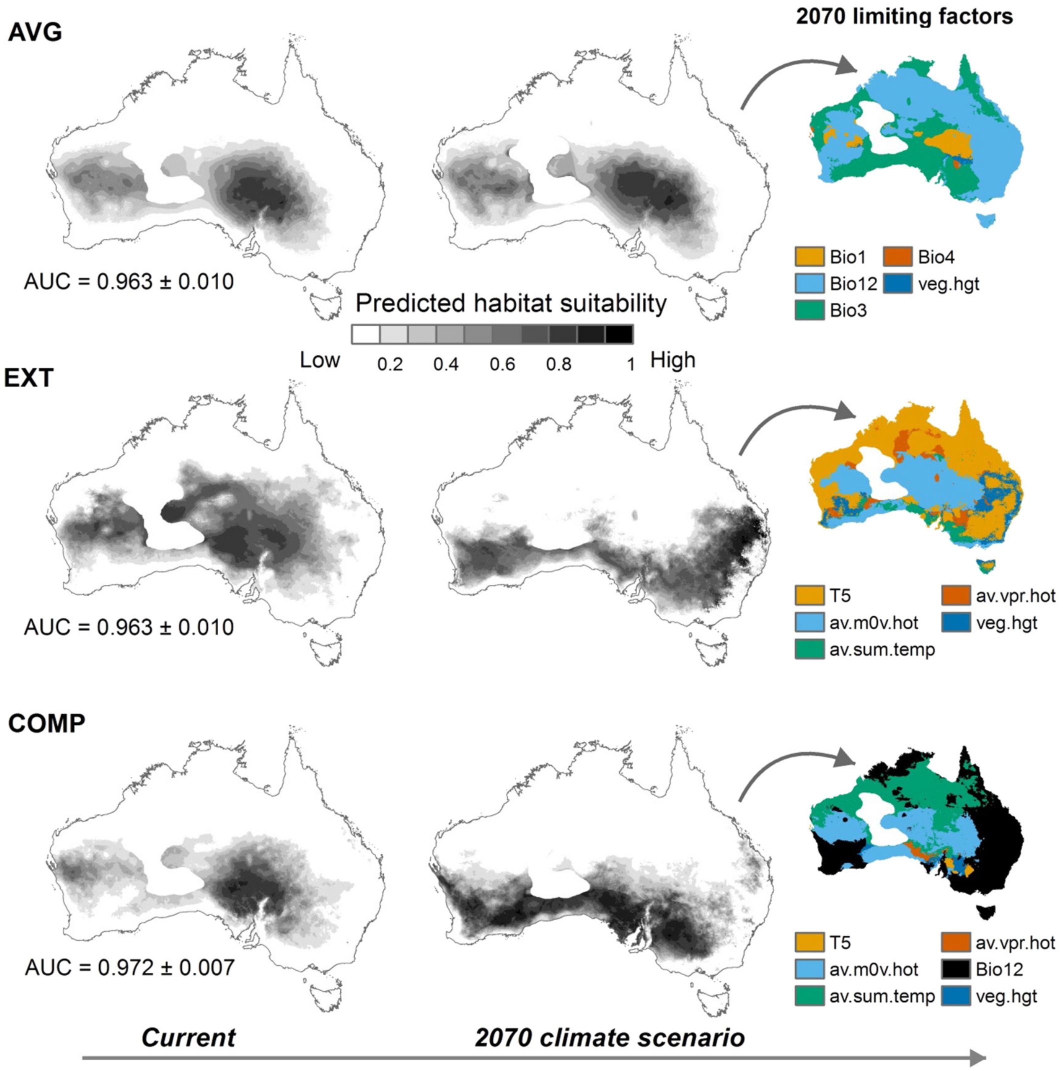

Figure 4. Environmental suitability maps for the paucident planigale *Planigale gilesi* as predicted by each climate predictor set (AVG, EXT and COMP). Predictive performance values (cross-validated AUC value, mean ± SD) are indicated for the current predictions of each model. The figure shows the contrast between the predictions of each predictor-set under current and future (2070) climatic scenarios (maps on first and second columns, respectively). The limiting factors maps (third column) show the variable that it is limiting the most an increase in environmental suitability at each grill cell and across the study area under the 2070 scenario and for each climate predictor-set individually (AVG, EXT and COMP). Refer to Table 1 for meaning of the variables' abbreviations.

showed that species distribution models based on long-term averaged means and extreme conditions generally have similarly good predictive performance, and yet predicted geographic ranges for the same species often differ (both in extent and spatial distribution). Differences in the spatial predictions of these models increase under future climate scenarios (Fig. 4, Supplementary material Appendix 7). These differences are likely to have significant implications for conservation, such as leading to different spatial priorities for conservation actions, and in extreme instances, influencing extinction risk status assessment under IUCN red list or other prioritization approaches. Our results highlight the importance of accounting for extreme conditions/events alongside traditionally used long-term averaged climatic predictor when modelling species distributions on the basis of their climatic niche. Failure to consider the potential role of extreme conditions when modelling species distributions could lead to unreliable predictions of species responses to change in climate.

Across species, EXT and COMP models tended to predict more restrictive suitable ranges than AVG models suggesting that extreme weather conditions might limit species distributions in areas theoretically suitable in terms of long-term mean climatic conditions. In other words, models based on long-term averages might be over predicting the amount of environmental suitable area for a species, at least in some areas (Zimmermann et al. 2009, Reside et al. 2010, Bateman et al. 2012, 2016, Briscoe et al. 2016). Divergences

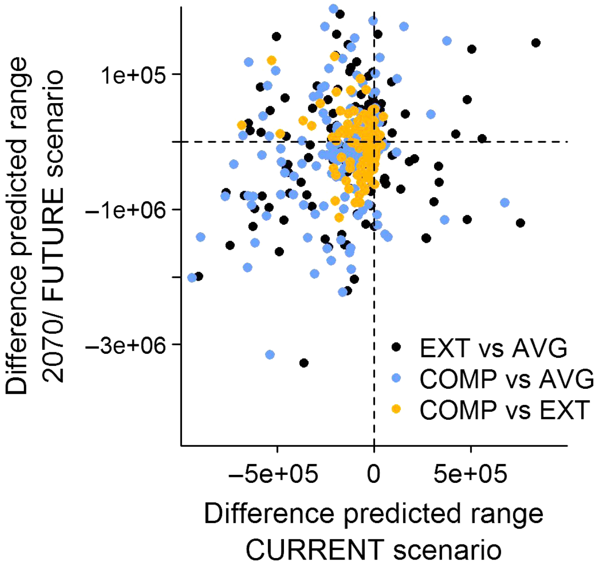

Figure 5. Differences in the predicted environmental suitability range between the three predictor-sets (AVG, EXT and COMP) for current climate scenarios (current scenario – x-axis) for a hot and dry climate 2070 future scenario (2070 scenario – y-axis). Environmental suitability range was calculated as the sum of grid values of the logistic MaxEnt output across Australia. When comparing EXT vs AVG, positive values in any of the axis indicate that the total range predicted by EXT models is larger than the range predicted by the AVG models, and negative values indicate the opposite. Similarly, for the COMP vs AVG and the COMP vs EXT comparisons. The intersection between the two dashed black lines represents a species for which there was no difference in predicted suitable range between models under either current or 2070 (future) scenarios.

between model predictions showed strong patterns in geographic and environmental space (Supplementary material Appendix 7), providing general insight into key processes that may be missed by failing to consider a broad suite of climate variables. Based on annual mean temperature values (AVG models) many species that occur in temperate areas along the east coast of Australia were predicted to also find suitable environmental conditions in the arid central parts of the continent and/or in the subtropical or tropical northern areas under the current climate scenario. Although these areas may not differ substantially in mean climate, they are likely to present quite different challenges to mammal species. For example, mammals that rely heavily on evaporative cooling may struggle to regulate their body temperature when faced with high temperatures coupled with high humidity – conditions that frequently occur in subtropical and tropical areas (Adolph 1947, West 2003, Briscoe et al. 2016). Similarly, the arid zones of central and northern Australia are challenging for species that do not have physiological or behavioural adaptations (e.g. heterothermy, use of burrows, nocturnality) to cope with long heatwaves or extended dry spells captured in the EXT model thorough the variables *av.sum.temp* and *av.m0v.hot* (Fuller et al. 2014). While we found no strong patterns between the divergence of predictions between different models and a number key species' traits, we did find that range predictions in the future tended to diverge more for species that occupied environments characterised by these conditions (e.g. desert and areas with hot summers/ mild winters).

Models based on extreme conditions only (EXT) predicted higher suitability for species than AVG models in areas of very high annual rainfall (mainly areas corresponding to the distribution of rainforest in Australia) and areas characterized by low minimum (temperatures below 5th percentile) and average annual mean temperatures. This might be due to the fact the variables included in the EXT model focused on capturing extreme conditions that are likely to prove physiologically challenging for mammals. These variables may fail to capture processes responsible of the distribution of vegetation communities and their productivity over space and time (which in turn determine patterns of species distributions and richness), such as the cumulative effect of rainfall over time in combination with annual mean temperatures (Huston and Wolverton 2009). These factors were better captured in the AVG model (annual mean temperature is known to be a good proxy for net primary productivity; Gaston 2000, Huston and Wolverton 2009) and therefore in their absence, EXT models might have overestimated the suitability of some areas for many species. For example, mountain areas in the southeastern Great Dividing Range will have similar values of T5 (extreme minimum temperatures) than neighbouring temperate or semi-arid inland areas, yet their annual mean temperature and total rainfall – and therefore the vegetation communities and species they support – differ substantially (e.g. dense forest in the Great Dividing Range vs open dry woodlands). Ideally, both extreme conditions and long-term averages should be considered together as potential predictors for species distribution models (e.g. COMP models in this study), since each individual extreme and average climatic variable might help to capture different aspects of the ecology and distribution of the species over different spatial scales. This is supported by the fact that in our study, COMP models tended to perform slightly better than either EXT or AVG models (although we note that they did also have one extra predictor variable, which may have had a minor influence on results). However, there are potential drawbacks of integrating all these variables in the same model: many of the extreme weather conditions are strongly correlated to long-term averages under the current conditions (Supplementary material Appendix 2), and the inclusion of correlated variables might hamper the capacity of using these models for inference (James et al. 2013). Model averaging or ensemble modelling approaches may prove useful as a way of capturing multiple processes in inference and prediction (Wintle et al. 2003, Thuiller et al. 2009) while avoiding parameter instability during model fitting.

Correlations between extreme variables and average conditions are expected to change over space and time: recent studies have demonstrated that extremes of temperature and precipitation are changing at a faster rate than annual trends (Alexander et al. 2007). This might help explain why spatial predictions – and therefore correlations – between different models diverged more under the future climatic scenario tested here than under the current climate. Divergence in EXT, COMP and AVG future model predictions is also associated with the fact that more than 50% of the extreme conditions predicted for 2070 showed non-analogue conditions under current climate (i.e. there is a large uncertainty of predictions in more than 50% of Australia). The extrapolation of predictions to non-analogue environmental conditions in MaxEnt is controlled by a feature called 'clamping': it constrains predictions to remain within the range of values of the training data (in the case of this study, the target-group background data set used to characterize the range of available environmental conditions under current climate) (Elith et al. 2011). Therefore, the prediction of environmental suitability in areas of non-analogue climate is constant. In our simulations, non-analogue conditions for EXT models were largely driven by longer runs of hot days (*av.m0v.hot*) than observed under the current climate. In many instances, the relative environmental suitability for species' was close to zero at the maximum values of *av.m0v.hot* under the current climate, supporting the use of the 'clamping' feature. These predictions do not explicitly take into account the physiological thresholds of the species (which in most cases is unknown as it requires detailed studies/lab experiments not available for most of the species; Krockenberger et al. 2012) nor the resilience and plasticity of the species to adapt to changes in environmental conditions (Elith and Leathwick 2009, Catullo et al. 2015). For example, model predictions for the species *Rhinonicteris aurantia*, the orange leaf-nose bat using EXT and COMP predictors sets showed that there would not be any climatic suitable conditions for the species in a hot and drier Australia in 2070 (Supplementary material Appendix 7). However, this species roosts in cave environments that are strongly buffered against daily, seasonal and long-term variations in external climatic conditions (i.e. environments with relatively constant temperature and humidity). Therefore, the 2070 predictions of EXT and COMP models might not correspond to the real conditions that the species will experience in a hot and drier climate future.

Our finding that models with apparently similar predictive performance when evaluated against current observation data can diverge so much when projected to future climates has significant implications for the way predictive uncertainty should be represented and results used in conservation decision making. The use of extreme weather variables known to directly impact species or groups of species (mammals in this case) when making predictions of future species ranges, permits identification of areas in the landscape where species will be more or less at threat by extreme weather. This helps identify future climatic refugia where species could be buffered against extreme events, providing greater chances of adapting to long-term changes in average climatic conditions (Reside et al. 2014). However, very few studies that analyse the long-term prospects for species under climate change account for the potential effect of extreme weather conditions. This may be partly due to the fact that, relative to data on future mean climate, projections of extremes (e.g. length of heatwaves or dry days) are much less commonly available (Garcia et al. 2014). The uncertainty arising from having to choose between models – e.g. model types or model predictors – is almost never represented as prediction uncertainty or formally considered when assessing conservation options (sensu Moilanen and Wintle 2006). Our results highlight the importance of incorporating uncertainty about predictor choice when representing SDM prediction uncertainty and interpreting the results of climate change impact studies. For several species in this study that appeared to be modelled quite well based on current data (high AUCs, high deviance reduction), the predicted 2070 distributions ranged from total loss of suitable range through to a substantial increase in range, depending on which climate or weather variables were included in the model. There remain significant challenges in interpreting and acting on such results that will require both further validation data (species presence–absence data – which is more robust than presence–only data for evaluating predictions, but rarely available at large spatial scales for most taxa) and sophisticated decision support approaches to explicitly factor in predictive uncertainty. It is well understood that choosing a single-best model for inference and prediction about the future of a species is a risky strategy (Wintle et al. 2003, Thuiller et al. 2009). We advocate for thoughtful application of multi-model inference and treatment of model-choice uncertainty when predicting the future distribution of a species and planning for the conservation of species in a rapidly changing world.

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Supplementary material (Appendix ECOG-02850 at <www.ecography.org/appendix/ecog-02850>). Appendix 1–9.