Nice weather for bettongs: using weather events, not climate means, in species distribution models

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Current applications of species distribution models (SDM) are typically static, in that they are based on correlations between where a species has been observed (ignoring the date of the observation) and environmental features, such as long-term climate means, that are assumed to be constant for each site. Because of this SDMs do not account for temporal variation in the distribution of suitable habitat across the range of a species. Here, we demonstrate the temporal variability in the potential geographic distributions of an endangered marsupial, the northern bettong *Bettongia tropica* as a case study. Models of the species distribution using temporally matched observations of the species with weather data (including extreme weather events) at the time of species observations, were better able to define habitat suitability, identify range edges and uncover competitive interactions than models based on static long-term climate means. Droughts and variable temperature are implicated in low densities and local extinctions of northern bettong populations close to range edges. Further, we show how variable weather can influence the results of competition with the common rufous bettong *Aepyprymnus rufescens*. Because traditional SDMs do not account for temporal variability of suitable habitat, static SDMs may underestimate the impacts of climate change particularly as the incidence of extreme weather events is likely to rise.

Species distribution models (SDMs) are increasingly used to characterize the ecological niches of species and to project those niches onto geographical space in order to predict species occurrences now or in the future (Guisan and Thuiller 2005, Araújo and Guisan 2006, Hijmans and Graham 2006, Jimenez-Valverde et al. 2008, Thuiller et al. 2008, Elith and Leathwick 2009, Fitzpatrick and Hargrove 2009). Typically, SDMs are a static representation of suitable habitat for a species (Franklin 2010) and do not account for temporal variation in habitat suitability (but see Reside et al. 2010). SDMs are often based on simple correlations between species occurrences and environmental features (Elith et al. 2006a), without reference to the date of occurrence, and environmental variables associated with a location are assumed to be constant.

This static approach may be valid for features such as substrate or topography which can reasonably be assumed constant, but problems arise when climate variables are entered into SDMs. Such variables are usually entered as long-term means (for example, 30 or 50 yr averages of mean annual temperature and precipitation) that describe a climate regime (Elith et al. 2006b), rather than as explicit measures that represent time-specific patterns of weather (but see Reside et al. 2010). This is a weakness, for two reasons. First, the long-term mean of a variable like temperature is an abstraction that tells us little about the temperatures that organisms actually experience through their lifetimes, or at stages of their lives that are crucial for fitness. Second, we know that occasional episodes of extremes of temperature, rainfall or other climate variables can have large impacts on the distribution and abundance of species (Parmesan et al. 2000, Brown et al. 2001, Korpimaki et al. 2004, Thuillier et al. 2008, Albright et al. 2010), but these extremes are not depicted by mean values (Zimmermann et al. 2009). In order to determine the main drivers of habitat suitability of a species, one may need to control for time scale so the importance of such extreme weather events in shaping a species distribution can be determined.

In addition, populations close to range boundaries are likely to be more sensitive to environmental change than those within the core (Anderson et al. 2009). Populations on the edge of the range are likely to be more vulnerable to extreme weather events, defined as episodes during which conditions move outside the range that an organism can endure (Gutschick and BassiriRad 2003). This is because they may be living close to the limits of their physiological tolerances (Parmesan et al. 2000, Thuiller et al. 2008, Brook et al. 2009). If a site becomes increasingly subject to episodes of unsuitable conditions for a species, such as when suitable climate conditions shift away from the present location within the trailing edge of a species range, traditional static SDMs will have low ability to represent this (Akçaakaya et al. 2006, Anderson et al. 2009). In addition, competition from invading species is also likely to have a more pronounced
negative impact within the trailing edge of a species range (Anderson et al. 2009) which could compound the problem of shifting suitable habitat in the short-term. As a result, traditional climate-based SDMs may have limited capacity to discriminate suitable from unsuitable sites now or in the future, such that species may be uncommon or absent in areas predicted to have high environmental suitability for them (Jentsch et al. 2007, Jentsch and Beierkuhnlein 2008). In other words, static SDMs represent a good depiction of where a species has occurred over an average of 30–50 yr, but are of little use when determining the persistence of a species through time in all parts of that range.

For all of these reasons, we hypothesize that including more dynamic information in SDMs to account for temporal variation, such as that produced by weather and extreme weather events, will a) better define short term habitat suitability than models based on long-term climate values, b) provide more precise information on the location of range boundaries (range edge versus core), and c) potentially allow better prediction of the outcome of competition between species. Additionally, we seek to determine if extreme weather events are important drivers of temporal variation in suitable habitat, and if range edges are more responsive than the range core to such events.

Methods

Study species

We tested these ideas using two marsupial species, the endangered northern bettong Bettongia tropica and its potential competitor, the rufous bettong Aepyprymnus rufescens.

The endangered species, the northern bettong, occurs only in a narrow band of habitat within the Australian Wet Tropics, where precipitation is high and the environment is suitable for its primary food source, ‘truffles’ (underground sporocarps of ectomycorrhizal fungi), while the generalist species, rufous bettong, occurs across a broad gradient of temperature and precipitation (Johnson and McIlwree 1997, Vernes 1999, Bateman 2010). Truffle availability is linked to short-term weather patterns (rainfall and temperature) that drive truffle fruiting events (Abell et al. 2006, Bateman 2010), and truffle availability in this region is highest in wetter habitat types (Vernes 1999). While both species feed on truffles and grasses, the persistence of the northern bettong may be linked to consistent availability of truffles (Johnson and McIlwree 1997, McIlwree and Johnson 1998), because truffles are the major diet item for most of the year. These two species are known to occupy the same areas within the drier end of the northern betttongs range. However, they appear not to co-occur at the same sites at the same time (Winter 1997, Bateman 2010), and there is one documented case of a shift from sole occupation of a site by the northern bettong to sole occupation by the rufous bettong. This happened between 2003 and 2006 at the southern edge of the northern bettong’s range (on the Coane Range; Fig. 1a) (Bateman 2010) where the northern bettong occurs in much lower densities than in the core of its distribution (on the Lamb Range; Fig. 1A) (Winter 1997, Vernes and Pope 2006). Earlier surveys in this area, in the late 1980s and early 1990s, failed to detect the northern bettong but recorded rufous bettongs inhabiting the area (Laurance 1997, Winter 1997). Although occasional fluctuations between northern and rufous bettongs are noted within the core population, these occur only at the western, drier edge of the northern bettong’s range in that area (Winter 1997, Vernes and Pope 2006). It is unknown what factors cause such population contractions and expansions of the two species.

Analysis

First, we tested if weather could provide a more accurate discrimination of suitable habitat than long-term climate means. Climate-only distribution models were developed for both the northern bettong and rufous bettong using Maxent (Maxent ver. 3.3.1) (Phillips et al. 2006) (Fig. 1) (adapted from Bateman 2010). Data used were occurrence records for the northern bettong (881 occurrence records, 326 unique location records) and rufous bettong (1343 occurrence records, 179 unique location records). All records were collected from the state of Queensland, Australia. Maxent was parameterized with default settings with the exception of the removal of threshold and hinge features. Background points were selected at random from regions represented by a 100 km species-specific buffer around the occurrence points, as in VanDerWal et al. (2009).

Climate variables, based on long-term climate means (1961–1990), were derived from ANUCLIM 5.1 software (McMahon et al. 1995) using monthly averages and an 80 m DEM re-sampled from ~250 m (GEODATA 9 second DEM ver. 2; Geoscience Australia, <www.ga.gov.au>). Variables were: mean annual temperature, temperature seasonality, maximum temperature of warmest period, minimum temperature of coldest period, annual precipitation, precipitation of wettest quarter, precipitation of driest quarter and precipitation seasonality.

Second, to examine the potential for weather to define range boundaries and the outcome of competition we defined extreme weather events in terms of the biological sensitivity of truffles within this ecosystem. Weather data were generated from the Australian Water Availability Project (AWAP) for the time period 1980–2008 (<www.bom.gov.au/jsp/awap>). Data consisted of daily precipitation and temperature values at ~5 km (0.05 degree) resolution, and summarized into 18 variables. Variables were selected to represent two kinds of extreme events in particular: droughts and heat waves. The thresholds used to define these events as ‘extreme’ were based on the biological sensitivity of relevant organisms (Gutschick and BasiriRad 2003). Drought events were defined as 14-d periods with < 50 mm rainfall. The 14-d criterion was used as it has been identified as the time period over which truffle production responds to weather, in particular rainfall (Claridge et al. 2000), and a rainfall threshold of 50 mm was chosen based on expert opinion that rainfall events of 50 mm or more are needed to trigger truffle fruiting in this region. Consecutive days with temperatures above 28°C are considered heat waves based on the upper limits of both truffle tolerances in the Wet Tropics (Bateman 2010) and temperature tolerances of bettongs (Seebeck and Rose 1988, Rose et al. 1990).
Summary weather variables included: maximum temperature (mean and standard deviation SD), minimum temperature (mean and SD), temperature range (mean and SD), and rainfall (mean and SD). The extreme events variables were: the number of heat waves (consecutive days above 28°C within the summarized period), the length of heat waves (mean and SD), total degree days above 28°C (measure of temperatures above 28°C), number of drought periods (consecutive 14 d periods with total rainfall below 50 mm), length of drought periods (mean and SD), and rainfall during drought periods (minimum, total, and daily). Variables were summarized for a period of five-years prior to the date of a presence/absence record to include any time lag that may occur between the event and its impact on a population.

Models were built for three cases to assess the impact of extreme weather events on short-term habitat suitability and competitive outcomes. These included the 1) northern bettong records from the core (Lamb Range) versus the southern range edge of its range (Coane Range), 2) northern bettong versus the rufous bettong, where both models were built using presence records as the binomial response and 3) northern bettong presence and absence at its southern range edge (Coane Range). The Coane Range was selected out of the sites from the range edges due to sufficient data availability (12 unique time/location presence records; from years 1997–1998, 2001 and 2003) and the accessibility of absence data (48 unique time/location absence records; from years 2006–2008) from comprehensive trapping surveys (Bateman 2010). Presence or absence records used in each model were associated with both location and date which was then used to identify the value for each weather variable prior to the presence/absence event (for each summarized time period). Species occurrence data, including spatial and temporal data, for the northern bettong (414 unique time/location presence records; from years 1981, 1983–1985, 1987–2005, and 2008) and rufous bettong (930 unique time/location presence records; from years 1980–2008) were obtained from field surveys and institutional databases. Records were obtained only for the period between 1980 to 2008, as this is when northern bettong records were consistently and reliably collected (Winter 1997).

Distribution models using weather data were built using generalized linear modelling (GLM). A Kullback–Leibler (K–L) information-theoretic method was used to construct all possible model configurations (best subsets) (Burnham and Anderson 2002). A binomial distribution was used to represent the occurrence records for model comparisons. The Bayesian information criterion (BIC) was used in model selection to account for sample sizes and penalize over-parameterisation (Burnham and Anderson 2002). Models were filtered using the variance inflation factor (VIF) set at a value of five, a more stringent value than the recommended value of 10, to remove models with highly correlated predictor variables (Zuur et al. 2010). After model filtering, models within seven BIC units (Δ) of the BICmin, the model with the lowest BICc value, were retained (Burnham and Anderson 2002).
Model averaging was conducted to determine the relative importance of each variable contributing to model building (Burnham and Anderson 2002). A measure of variable importance, or variable weight, was calculated by summing all of the weight scores (wi) for any model of which the variable was a component. The top variables with the top three variable weight scores were plotted in a 3-dimensional scatter plot. Top variables were then projected onto geographical space from 1980 to 2008 using daily weather information, summarized to monthly layers, for the region. Predictions were clipped to fit within predictions of suitable habitat, as given by a climate-based distribution model created in Maxent to exclude areas below 400 m altitude. This was done as northern bettongs are known to only occur above this altitude (Winter and Johnson 1995) and to compensate for coarse resolution of the weather data. It is important to note that 3-dimensional scatter plots of the weather space presented here are limited to only three variables and it is understood that additional variables could improve model resolution; this is forsaken here due to visual complexity. Regardless, some overlap in weather space may occur where similar conditions are experienced near range edges. All analyses were conducted in R (v2.10.0, <www.r-project.org>).

For both climate and weather based models, the AUC (area under curve; or the area under the receiver operating characteristic (ROC) curve) was used for model evaluation, with values above 0.5 are better than random predictions, and those above 0.7 considered useful (Elith et al. 2006a) and those above 0.9 highly accurate (Guisan et al. 2007). It is important to note that these AUC values are resubstitution accuracies only and may be over-optimistic (Fielding and Bell 1997).

Results

Long-term climate predictions

Habitats of high suitability for the northern bettong under current climate conditions are predicted, based on climate-only models, in several areas of the Wet Tropics bioregion (Fig. 1B). Additionally, the climate-only SDMs indicated high suitability and niche overlap between northern and rufous bettongs (Fig. 1B,C). Top variables for the northern bettong climate-only model (AUC = 0.989) were annual mean temperature (25.9%), maximum temperature of the warmest period (21.2%), and temperature seasonality (15.6%). Top variables for the rufous bettong climate-only model (AUC = 0.989) were annual mean temperature variability (wi = 0.83), daily rainfall of drought periods (wi = 0.11), and rainfall variability (wi = 0.09). Top variables for the comparison of northern bettong to rufous bettongs were temperature variability (wi = 0.1), rainfall variability (wi = 0.99), and average maximum temperature (wi = 0.98), although total degree-days above 28°C (wi = 0.95) and maximum temperature variability (wi = 0.94) were also important. For northern bettong presence and absence, the top variables were the number of drought periods (wi = 0.34), average rainfall of drought periods (wi = 0.31), and average rainfall (wi = 0.29).

There were distinct differences in the weather of the core of the northern bettong range (Lamb Range; high density northern bettong populations) and the southern range edge (Coane Range) (Fig. 2). Top variables from generalized linear model outputs gave complete discrimination between populations (AUC = 1.0). In the south, minimum temperature was more variable and drought periods had lower daily rainfall than in the core of the range; that is, weather was more variable and droughts more harsh. The core population on the Lamb Range had higher daily rainfall, and rainfall was also more consistent during low-rainfall periods. Minimum temperature variability (wi = 0.83), daily rainfall of drought periods (wi = 0.11), and rainfall variability (wi = 0.09). Top variables for the comparison of northern bettong to rufous bettongs were temperature variability (wi = 0.1), rainfall variability (wi = 0.99), and average maximum temperature (wi = 0.98), although total degree-days above 28°C (wi = 0.95) and maximum temperature variability (wi = 0.94) were also important. For northern bettong presence and absence, the top variables were the number of drought periods (wi = 0.34), average rainfall of drought periods (wi = 0.31), and average rainfall (wi = 0.29).

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Using weather to build distribution models

All models built using weather performed well (Table 1) indicating models were useful and highly accurate. Top variables from model averaging are presented here, while the entire set of candidate models are presented in supplementary material (Supplementary material Appendix 1, Table A1). For the northern bettong core versus edge, the top variables were

<table>
<thead>
<tr>
<th>Model scenario</th>
<th>Average AUC</th>
<th>SD</th>
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<tbody>
<tr>
<td>NB core vs NB southern range edge</td>
<td>1.0</td>
<td>0.00</td>
</tr>
<tr>
<td>NB vs rufous bettong</td>
<td>0.97</td>
<td>0.001</td>
</tr>
<tr>
<td>NB presence vs NB absence</td>
<td>0.99</td>
<td>0.02</td>
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Figure 2. Top variables based on GLM outputs for northern bettong core versus southern range edge records. The core is the Lamb Range and the southern range edge (margin) is the Coane Range. Records are indicated as those accurately predicted (northern bettong core (core +) in red, southern range edge (margin +) in blue) and those inaccurately predicted (northern bettong core (core –) in black, southern range edge (margin –) in yellow). If no inaccurate predictions were made, black and yellow will not be represented on the plot.
temperatures were less variable. This evidently represents ‘good northern bettong weather’ given the higher abundance achieved on the Lamb Range.

Weather conditions did not discriminate conditions associated with occurrences of northern and rufous bettongs quite so clearly. Although the species occupy separate regions of the environmental space defined by our weather variables, there was a narrow overlap zone between them (Fig. 3). The rufous bettong occurred where minimum temperature was more variable and rainfall less variable, with higher maximum temperatures (AUC = 0.97). The top model (Supplementary material Appendix 1, Table A1) for northern bettong versus rufous bettong included minimum temperature variability, rainfall variability, average length of heat waves, average length of drought, and daily rainfall of drought indicating that, although extreme weather events are not captured in the top variables, the most parsimonious model did contain them.

Comparing presence and absence records of the northern bettong at the southern range edge (on the Coane Range) revealed a clear separation in weather (Fig. 4; AUC = 0.99). Absence records were associated with longer drought periods (less ‘dry clusters’ of longer duration) indicating prolonged periods with consecutive 14-d periods of < 50 mm rainfall. Absences also had higher total rainfall within drought periods, but this is a product of having longer consecutive dry periods as the measure was of rainfall across the entire drought. Presence records were associated with shorter and more variable drought periods, often with intense drought periods (low rainfall within drought periods) but which were not prolonged. Average rainfall over each five-year period was higher when northern bettongs were present than when they were absent.

Figure 4. Top variables based on GLM outputs for northern bettong presence and absence in the southern range edge. The southern range edge is the Coane Range. Records are indicated as those accurately predicted (absence (nb.a +) red, presence (nb.p +) in blue) and those inaccurately predicted (absence (nb.a –) in black, presence (nb.p –) in yellow). If no inaccurate predictions were made, black and yellow will not be represented on the plot.

Weather models in geographical space through time

Reconstruction of weather patterns through space and time suggest that the northern bettong and rufous bettong are in a dynamic relationship with each other (Supplementary material Appendix 2, Video–A2). Regions identified as highly suitable from climate only models (Fig. 1) at the range edge of the northern bettong distribution showed variation through time in weather suitable for that species. Fluctuations in weather in this environmental space lead to alternations between conditions suitable for northern and rufous bettongs. Suitable weather conditions for each species oscillate through time over the whole Wet Tropics region, with temporal expansions and contractions of suitable weather for each species observed. These expansions and contractions occur in proximate relation to each other, with a narrow overlap zone where competitive interactions are likely to take place. In geographic space, this overlap zone is more pronounced within the southern edge, where complete shifts between suitable weather for each species are observed. Within the core of this species range, the overlap zone between northern and rufous bettongs is minimal, and occurring at the western, drier portion of northern bettong range.

Suitability of weather for the northern bettong, as indicated by weather conditions in the core of the distribution, also fluctuated through time (Supplementary material Appendix 3, Video_A3). This oscillation of suitable weather varied across the distribution predicted for the species from the climate-only model. Sometimes the core area and range edges have similar weather conditions with connectivity established throughout the Wet Tropics. At other times the distribution of suitable weather contracted, especially due to increased drought and amplified temperature variability at
range edges. This fragmented the potential distribution of the species.

Data from the southern range edge for particular time slices show how changes in weather have affected populations at the edges of the species range. Trapping surveys revealed that in October 1997 northern bettongs were present within the southern range edge, but by May 2006 they could not be detected despite considerable trapping effort, and had been replaced by the rufous bettong (Bateman 2010); evidently the local distribution of the northern bettong had contracted and the population decreased in abundance (Fig. 5). Northern bettong presences in the southern range edge coincide with weather conditions matching that of the core population (Lamb Range). This was also supported by geographical depiction of the interaction between northern and rufous bettongs and weather (Fig. 6). In October 1997 much of the Wet Tropics is indicated as experiencing weather consistent the overlap zone between these two species. By May 2006, however, weather conditions are more suitable for rufous bettongs over much of the Wet Tropics including the southern range edge.

Discussion

Despite knowledge to the contrary, many exercises examining the distribution and abundance of species (including correlative SDMs as used here) make an assumption that species are in equilibrium with their environments (Pearson and Dawson 2003); we highlight the inappropriateness of this assumption here. We show a system of temporally variable weather, where short-term weather conditions appear to be driving spatial patterns of distribution and abundance for these two bettongs. Here, we show the approximate set of climate conditions, or in this case weather conditions, in which a species can occur (the Grinnellian niche; Soberón 2007) do change in geographical space and fluctuate across the landscape on the short-term. Particularly within the range edge for the northern bettong, these changes have induced niche tracking for these bettong species; that is when species, limited by physiological boundaries, follow their favourable environmental conditions (niche) through geographical space or face local extinction within their present range (Tingley et al. 2009). Although the climate-based distribution model

Figure 5. GLM weather models in geographical space in different time slices for the core versus the southern range edge. The core, Lamb Range, represents ‘stable northern bettong weather’ represented by red here and the southern range edge, the Coane Range weather, is represented by green: (A) October 1997 when northern bettongs were present in the southern range edge; (B) May 2006 when northern bettongs were not detected in the southern range edge. See full animation in supplementary material (Supplementary material Appendix 2, Video_A2).
due to extreme heat or drought have been noted in the trailing edge of species ranges, and the effects of competition can be amplified during such times (Gutschick and BassiriRad 2003, Anderson et al. 2009, Zimmermann et al. 2009). This is because the impacts of biotic interactions are likely to be greatest close to the range limits of a species, where expansions and contractions of distribution of interacting species occur in response to changes in weather (Davis 1986, Anderson et al. 2009). The core region of the northern bettong consistently had less severe droughts and less variable temperatures, and weather conditions tended to be unsuitable for the rufous bettong. The stability of favourable weather and the suitability of the long-term climate of this region (Williams and Middleton 2008), coupled with less pressure from competitive interactions, can explain why northern bettongs reach their highest abundance there.

Despite arguments that competitive interactions are implicit in SDM outputs (Davis et al. 1998, Guisan et al. 2002, Kearney and Porter 2004, Sinclair et al. 2010) as records are taken from a species realized niche, we show here that unless temporal variation is included this is not the case. In our study, climate based SDM failed to recognize competitive interactions between two species, because the use of spatial data with no temporal component was not sufficient of the northern bettong reasonably reproduced the 30-yr range of the species, it did not account for the dynamics of suitable habitat within this range over time. Short-term weather events determined that range boundaries (core versus edge) experienced greater fluctuations in short-term weather suitability and provided insight into why some areas predicted from climate-based models to have high suitability for the northern bettong do not, in fact, support high density, stable populations.

Both weather and extreme weather events identified range boundaries as areas with high variability in weather and fluctuations in suitable weather conditions for the endangered northern bettong. In particular, extreme weather events which could be shown to better determine the range edge for the northern bettong, as well as its absence within this edge habitat. The importance of extreme weather events and their influence on temporal variation in suitable habitat of a species can be overlooked when climate models based on long-term means are used to characterize the distribution of a species, as the impacts of extremes are smoothed out and muted (Zimmermann et al. 2009). Organisms at their range limits are often most affected by extreme events like droughts, as they are likely to be already close to the limits of their physiological tolerances (Parmesan et al. 2000, Archaux and Wolters 2006). Range contractions of the northern bettong reasonably reproduced the 30-yr range of the species, it did not account for the dynamics of suitable habitat within this range over time. Short-term weather events determined that range boundaries (core versus edge) experienced greater fluctuations in short-term weather suitability and provided insight into why some areas predicted from climate-based models to have high suitability for the northern bettong do not, in fact, support high density, stable populations.

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to identify that these species do not co-exist in time. Here, competitive outcomes between species evidently tracked short-term weather; therefore weather data are needed to make predictions on where and when species are likely to occur. Niche tracking was observed between the competing bettong species, with temporal changes in suitable weather conditions fluctuating across the landscape. Shifts in a species range are likely to occur where changes in the climate space have occurred (i.e. increasing weather variability and extreme weather events) and/or where pressure from competition varies through time (Nogués-Bravo 2009). Although none of the top variables in the comparison between northern and rufous bettong weather contained an extreme weather event, the top models and other important variables did include heat waves, droughts, and degree days above 28°C indicating that both weather and extreme weather events are important drivers of temporal variation in both species. Time lags of five years were used in this study, so that the necessary length of time was needed for the effect of an event to be noticeable in fluctuations between these populations.

Periods of severe drought and variable temperatures presumably affected northern bettong populations through the decrease of truffle productivity. Truffles are particularly sensitive to environmental changes and abiotic stress (Bougher and Lebel 2001, Brown et al. 2001) and are not consistent in the environment at all times (Abell et al. 2006, Bateman 2010). Truffle reproduction is strongly linked to both rainfall and temperature, and truffle availability is low during drought; that is truffles are a stochastic food resource that would not be well represented in SDMs by long-term climate means. More stable weather, with less severe droughts of shorter duration, would ensure continuous truffle availability as truffles in this region have a 1–2 month lag in response to rainfall events (Abell-Davis 2008, Bateman 2010). Weather conditions at the core of northern bettong habitat are sufficiently stable to provide a consistent supply of truffles as a food resource. In marginal habitats, truffle productivity is presumably more variable and northern bettongs would need to contract to wetter areas, tracking suitable conditions where truffles may persist (Johnson and McI1avee 1997). Species abundances are often dictated by the indirect impact of weather through the regulation on food resource availability (Lewellen and Vessey 1998, White 2008). Specialization may confer a competitive edge where resources are abundant and particularly within the core of suitable climate (Rosenzweig and Lomolino 1997, Ritchie et al. 2009). If the abundance of this resource diminishes or its suitable habitat contracts, than this competitive edge may be lost. Extreme population contractions, range shifts or potential local extinctions could occur if unsuitable conditions persist (Parmesan et al. 2000) and are coupled with competition and resource limitations (Brown et al. 2001).

This study shows that models using long-term climate means may underestimate the impacts of climate change on species distribution due to over-prediction of high suitability in marginal areas that often have unfavourable weather (Reside et al. 2010). The synergistic effect of extreme weather and habitat fragmentation adds to this problem (Laurance and Williamson 2001, Piessens et al. 2009). With extreme weather events predicted to increase (Jentsch et al. 2007), information on how such events affect species now should help us prepare for changes in climate in the future. Failure to address temporal dynamics of weather (including extreme events) in SDMs may lead to underestimation of the impacts of climate change, and result in misinformed conservation planning. In order to make meaningful predictions in the face of climate change and facilitate pre-emptive conservation planning, extreme weather events will need to be assessed in research on species distribution modelling to identify the areas of highest conservation priority.

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Supplementary material (Appendix E6871 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.


