



Correlative and mechanistic models of species distribution provide congruent forecasts under climate change

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Abstract

Good forecasts of climate change impacts on extinction risks are critical for effective conservation management responses. Species distribution models (SDMs) are central to extinction risk analyses. The reliability of predictions of SDMs has been questioned because models often lack a mechanistic underpinning and rely on assumptions that are untenable under climate change. We show how integrating predictions from fundamentally different modeling strategies produces robust forecasts of climate change impacts on habitat and population parameters. We illustrate the principle by applying mechanistic (Niche Mapper) and correlative (Maxent, Bioclim) SDMs to predict current and future distributions and fertility of an Australian gliding possum. The two approaches make congruent, accurate predictions of current distribution and similar, dire predictions about the impact of a warming scenario, supporting previous correlative-only predictions for similar species. We argue that convergent lines of independent evidence provide a robust basis for predicting and managing extinctions risks under climate change.

Introduction

Climate change will produce novel environments and ecosystems, presenting scientists with serious challenges in forecasting the impact on biodiversity (Fitzpatrick & Hargrove 2009). All potential management actions will require substantial public investment and it is thus imperative that the most robust methods be used to evaluate and predict the consequences of the range of management options available. Here, we present a robust prediction strategy to investigate the susceptibility of individual species to climate change. Our approach relies on using independent lines of evidence to derive species distribution models (SDMs) with which to forecast potential range shifts: (1) mechanistic SDMs based on functional traits and physiological constraints and (2) correlative SDMs relating occurrence data to spatial environmental data. Our approach is based on the premise that convergence of independent lines of evidence conveys

robustness to prediction and confidence to management strategies.

Mechanistic SDMs explicitly incorporate processes that limit distributions (Kearney & Porter 2009). All species have physiologically based environmental constraints that influence their distribution and abundance and these physiological processes are strongly tied to flows of mass and energy as individual organisms interact with their environments. It is through such processes that the impacts of climate change on biodiversity are propagated to higher levels of organization such as populations, communities, and ecosystems. The field of biophysical ecology provides a basis for calculating the physiological consequences of different environmental conditions on landscape scale as a function of climate, vegetation, and terrain, and so to develop mechanistic models of range limits independent of a species' present range (Porter *et al.* 2002; Kearney & Porter 2004; Buckley 2008; Kearney *et al.* 2008; Kearney & Porter 2009). Because

physiologically based SDMs explicitly include known processes in the model, they can be used more confidently to predict climate change impacts. The strength of such inferences, however, depends on identification of key limiting processes.

Correlative SDMs are widely used to predict the spatial distribution of species and impacts of climate change (e.g., Thomas *et al.* 2004). They exploit the statistical association between spatial environmental data and occurrence records to capture implicitly processes limiting the distribution of the species. Techniques for fitting SDMs have developed rapidly over the past 20 years (Guisan & Thuiller 2005; Elith & Leathwick 2009). Correlative SDMs convey practical advantages over more mechanistic modeling methods due to the simplicity and flexibility of their data requirements, their relative ease of use within freeware packages, and the range of the interactions (biotic and abiotic) they can detect and characterize. Consequently, correlative SDMs have been used widely in conservation applications (e.g., Moilanen & Wintle 2007).

Climate change is likely to produce novel environmental scenarios and nonequilibrium species distributions. The use of correlative SDMs in these contexts is considered precarious (Davis *et al.* 1998; Dormann 2007; Fitzpatrick & Hargrove 2009). Correlative SDMs are also local analyses (to the environmental space from which they are derived) that implicitly capture many ecological processes in the relationship between occurrence data and spatial information. When they are used to make predictions to unsampled environmental space, one assumes that all of these hidden processes are preserved in the new sample space. There are attempts to reduce this problem through ensemble methods that average across many different modeling approaches and data treatments (Araújo & New 2007). Yet this does not escape the qualitative nature of the information used for the predictions, that is, occurrence data, and the potentially complex and nonlinear ecological processes that they reflect.

An alternative approach is to base inference on qualitatively different and independent sources of information, that is, species distribution records and functional traits of the species. We take such an approach in this study and apply a mechanistic (Niche Mapper) and two correlative models (Maxent and Bioclim) to predict the distribution and fertility of folivorous Australian possums under current and possible future environmental conditions. We parameterized our models specifically for the greater glider, *Petauroides volans*, a widespread species that is well studied physiologically and is threatened by habitat loss and fragmentation across much of its range (Tyndale-Biscoe 2005). We assess the congruence of these independent predictions of the impact of climate change on

the greater glider and therefore the robustness of the inference.

Methods

Mechanistic SDM modeling and data

Greater gliders are nocturnal specialist feeders on *Eucalyptus* leaves, sheltering in tree hollows during the day. For the mechanistic SDM, we solved energy- and mass-balance equations for greater gliders and their diurnal retreats to calculate their energy and water requirements as a function of thermoregulatory and activity costs, using the Niche Mapper system (for a detailed description of this model, see Porter & Mitchell 2006) with parameters defined in Table 1. The solution for metabolic rate was not allowed to fall below the empirically observed basal rate plus the heat increment of feeding (Table 1). In such cases, animals were simulated to invoke the following thermoregulatory responses, in order, based on empirical observations (Rubsamen *et al.* 1984): (1) alter posture (uncurl), (2) increase thermal conductivity of the flesh, (3) allow T_{core} to rise, and (4) lose heat by evaporative cooling (panting and licking fur), up to an equivalent maximum of 30% of the surface area being wetted (equivalent to their response to 35 °C in a metabolic chamber) (Rubsamen *et al.* 1984).

During daylight hours, gliders were initially simulated to shelter in a tightly fitting, thin-walled tree hollow (Table 1), for which a steady-state solution was solved. Shade on the shelter was increased if the physiological thermoregulatory responses of the possums (see above) were unable to maintain the core below 39.1 °C under the maximum allowable evaporative cooling. In the frequent situation where conditions inside the above-described shelters were too hot, possums were assumed to use shaded hollows in trees with sufficient thermal inertia that daily temperature fluctuations were completely dampened and the ambient temperature was at the monthly mean temperature for that location. Tests of model predictions against empirical data (for metabolic rate, water loss rate and shelter temperatures) are presented in the Supplementary online materials, Figures S1–2).

Food (*Eucalyptus* spp. leaves) was assumed to always be available to active gliders and feeding rate was assumed to be constant throughout the night. To model the potential distribution of the greater glider based on these calculations, for each site we subtracted the thermally imposed energy and water costs from the income through the food, integrated across the year. This “discretionary” energy and water was then converted to milk based on the most limiting factor (energy, water, or protein), and

Table 1 Parameters for the mechanistic model of the greater glider's potential range. Pelt measurements were based on three individuals from the Central Highlands region of Victoria.

Parameter	Value	Source
Fur properties	Diameter: 9 μm Length: 30 mm Depth: 25 mm (dorsal), 5 mm (ventral) Density: 12,000/cm ² (dorsal), 13,000/cm ² (ventral)	This study
Mass	0.8 kg or 1.3 kg	(Tyndale-Biscoe & Smith 1969; Comport <i>et al.</i> 1996)
Shape	Ellipsoid, with eccentricity $E = ((A^2 - B^2)^{1/2})/A$ where, $B = C = (((3/8) * \text{volume})/\pi)^{1/3}$ $A = \text{curl} * B$ Curl = 3.5 or 4.0	Default values
Core body temperature	35.4–39.1 °C	(Rubsamen <i>et al.</i> 1984)
Flesh thermal conductivity	0.6–4.21 W/m per °C	Default values
Respiratory system	Oxygen extraction efficiency: 20%	Default value
Nest properties	Dimensions (cylinder, L × D): 1 m × 0.35 m Wall thickness: 0.05 m Thermal conductivity: 0.35 W/m per °C Wind speed: 0.1 m/s Relative humidity: 99%	Default value
Food properties	Protein: 1.4% dry mass Carbohydrate: 70.0% dry mass Lipid: 25.8% dry mass Dry matter: 48.7%	(Kavanagh & Lambert 1990) (Foley 1987; Foley <i>et al.</i> 1990)
Digestive system	Feeding rate (dry matter): 3.54 g/kg per hour Digestive efficiency: 48% Faecal water: 10% Urea in urine: 20%	(Foley 1987) Default value Default value
Metabolism	Basal metabolic rate: 2.37 W/kg Heat increment of feeding: 0.44 W/kg Activity cost: 1.48 W/kg	(Foley <i>et al.</i> 1990)
Milk composition and growth efficiency	Protein: 5.6% wet mass Carbohydrate: 8.5% wet mass Lipid: 2.2% wet mass Water: 80.5% Energy content: 4.39 kJ/g Milk conversion efficiency: 28%	(Munks <i>et al.</i> 1991) (Munks & Green 1997)

then into grams of offspring that could be weaned, using milk composition and growth efficiency data for the related species *Pseudochirus peregrinus* (Munks *et al.* 1991; Munks & Green 1997) (Table 1). Assessments of water balance assumed all water entered the body via the food or via metabolic water. Greater gliders have not been observed to voluntarily leave their arboreal environment but they may drink water on leaves and in tree hollows (Foley *et al.* 1990). We further distinguished water limitation, however, by determining areas where monthly water balance was predicted to be negative at times of minimal (<10 mm) rainfall.

Environmental conditions were estimated with a microclimate model (Porter *et al.* 1973; Porter & Mitchell

2006), driven by 0.05° resolution interpolations of monthly maximum and minimum values of air temperature, humidity, and wind speed, as well as mean monthly cloud cover, averaged over 30 years (Kearney & Porter 2004). Air temperatures were corrected to a 9'' DEM using an adiabatic lapse rate of −5.5 °C per km elevation increase.

Correlative SDM methods and data

A national database of spatially referenced sighting records for Australian native flora and fauna (see Slatyer *et al.* 2007) combined with records contributed by Eyre (2006) provided 6,729 recorded sightings of the greater

gliders. This data set samples close to the full spatial extent of *P. volans* in Australia. These were filtered to 6,323 records by removing “old” records (earlier than 1970) and records with a spatial accuracy of less than 200 m.

We obtained national-level coverage of a range of environmental variables at 9'' grid cell resolution that were thought to represent ecological processes likely to influence the spatial distribution of the gliders. Denning and nutritional requirements were modeled using a coarsely categorized map of the dominant vegetation cover obtained from aerial photo interpretation (National Forest Inventory 2003), broken into 10 categories based on structural (height and degree of canopy closure) and compositional classes (Supplementary material S3). We used 9'' grid cell resolution data for mean annual temperature, mean temperature of the coldest period, mean temperature of the hottest period, hottest temperature of the hottest period, and coldest temperature of the coldest period (Hutchinson *et al.* 2000). Mean rainfall of the wettest period, mean rainfall of the driest period, and soil fertility maps were used to characterize influences of environmental productivity on the nutritional suitability of locations for greater gliders.

The national-level greater glider observation database contains “presence-only” data so we used the freeware package “Maxent (3.1)” (Phillips *et al.* 2006) and “Bioclim” as implemented in the software package “DIVA-GIS 5.2” (<http://www.DIVA-GIS.org>). Default parameter settings were used for the Maxent and Bioclim models, including the use of the whole continent for the generation of pseudoabsence zeros for the Maxent analysis. We used Maxent’s *k*-fold cross-validation routine to provide a quasi-independent verification of the models’ “out-of-sample” predictive ability (Vaughan & Ormerod 2005; Hastie *et al.* 2009). We used a 10-fold cross-validation, which holds out 10% of the data as a testing set at each of 10 iterations, building the model on the remaining 90% of the data in each iteration. Out-of-sample predictive accuracy is assessed using the area under the Receiver Operating Curve (ROC) (Swets 1988). ROC areas are generally calculated on presence/absence data. However, in our case, the cross-validation procedure in Maxent utilizes true presences and pseudoabsences to generate the ROC statistics. This is akin to testing the ability of the model to correctly rank presences higher than “random” locations (all locations that are not known to contain a presence observation). The implication of this is that the true maximum value for any particular data set is unknown, though a very high ROC score still indicates a relatively good model. The value of area under the (receiver operating) curve (AUC) = 0.5 still holds the same interpretation when presence/pseudoabsence data are used to generate ROCs (Phillips *et al.* 2006).

Results

Mechanistic model

Milk production was maximal for the smaller body size in northern and inland parts of the range, and for the larger body size in southern parts of the range (Figure 1a). For all subsequent landscape-scale calculations, we allowed body size to take whichever of the two values was optimal for a given location. Reproduction (milk production) was limited in the northern and inland extremities of the range by water (Figure 1b). Regions close to the northern limit of the greater glider were limited in particular by water balance in September, when possums were in negative balance but were unlikely to find drinking water because of low (<10 mm) rainfall. Energy was limiting in the highland areas of south eastern Australia and protein was limiting across much of eastern and southern Australia (Figure 1b), including virtually all sites within the present range of the greater glider (Figure 2).

The estimated fundamental niche of the greater glider across Australia, assuming the uniform presence of food and shelter (i.e., tall eucalypt forest), maps to a large fraction of eastern Australia as well as the entire south coast and inland 100–800 km (conservatively assuming a weaning size of 500 g (Tyndale-Biscoe & Smith 1969)) (Figure 1c, see also Figures 3a and 4a). The estimated fundamental niche of the greater glider also maps much of Tasmania, excluding regions above 500–600 m and southern coastal areas. Climatically suitable parts of central southern Australia lack tall forest cover, however, and would thus be unsuitable (Figure 1d).

The final predicted range, excluding regions without tall forest, is presented in Figure 2a. In Figures 1a, 2, and 4, and in the comparisons of predicted habitat suitability between Niche Mapper and Maxent, we only constrained offspring production by energy or water production, not protein. This is because we have no data on spatial variation in protein availability.

Correlative model

The Maxent model, based on mean annual temperature, precipitation of the warmest quarter, and dominant vegetation type, provided good “out-of-sample” predictive performance for the current distribution of the species (ROC area = 0.98), according to the bootstrap model verification method. The bootstrapped ROC areas presented here are relevant only to the scale at which this analysis was undertaken (in this case, continental) and do not guarantee a similar predictive performance at a finer scale (Elith & Burgman 2002). Similarly, while strong ROC values imply good predictive performance for the

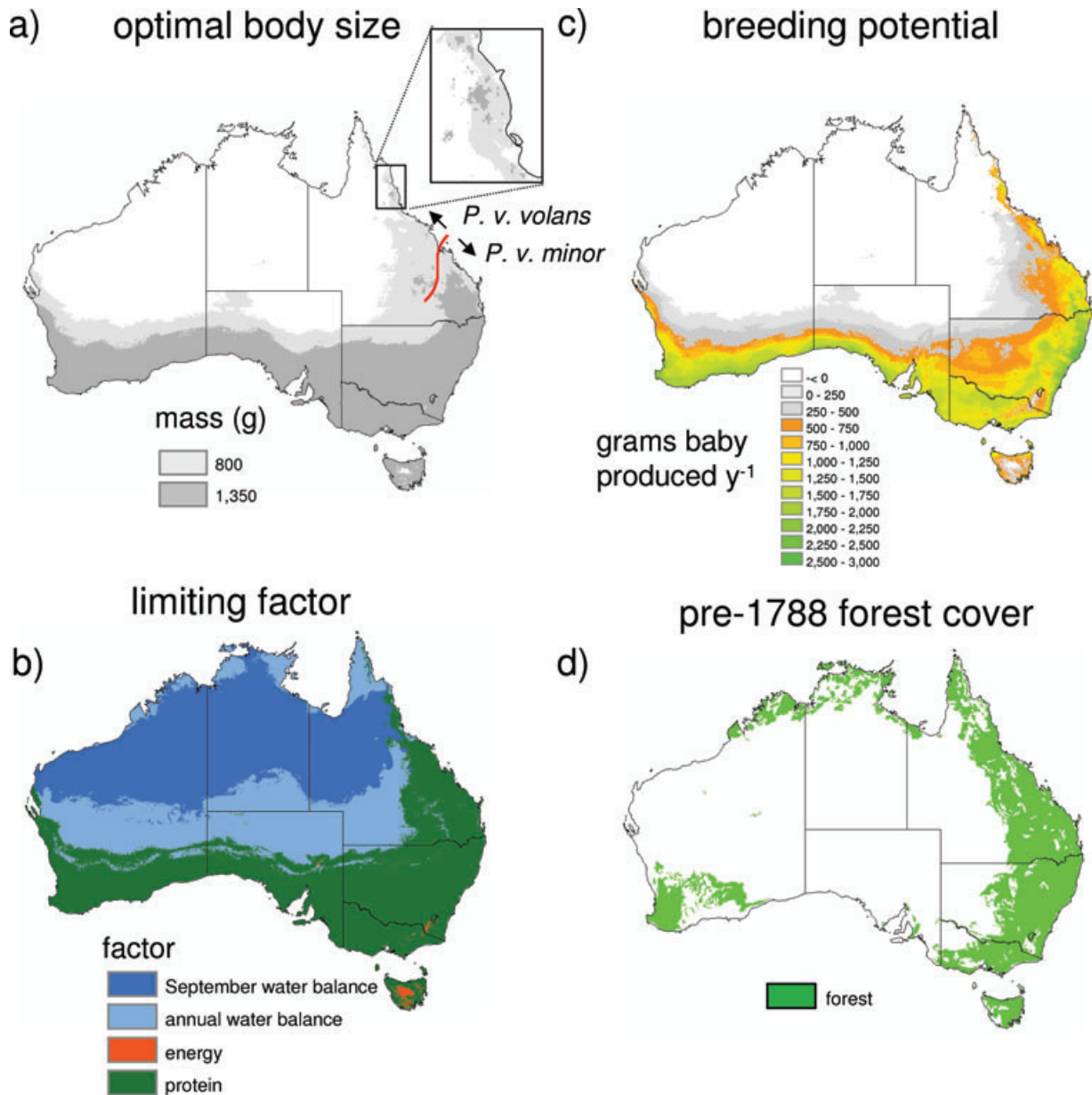


Figure 1 Subcomponents of the mechanistic species distribution model of the greater glider *Petauroides volans* developed in the present study, showing a) the optimal body size chosen by the model, given the choice between the putative mean size of the northern (*P. v. minor*) and southern

(*P. v. volans*) subspecies, b) the limiting factors inferred by the model, c) the predicted breeding potential as a function of energy and water income and expenditure and d) the distribution of tall forest habitat.

current range of the species (at a continental scale), that does not imply good predictive performance of the future range of a species, especially under climate change (Araújo *et al.* 2005). Alternative models containing more predictor variables provided little improvement in ROC area and generated almost identical predictive surfaces. Because the simpler model provided equivalent fit and predictive performance, we use it in preference to the

more complex competing models, for comparison with the physiological model. The correlative model maps well to occurrence data (Figure 2b), despite being fitted to only three predictor variables (the Bioclim model provided extremely similar results, see Figures. S4 and 5). This indicates that the fundamental drivers (temperature, rainfall, vegetation) explain the broad distribution of the species well.

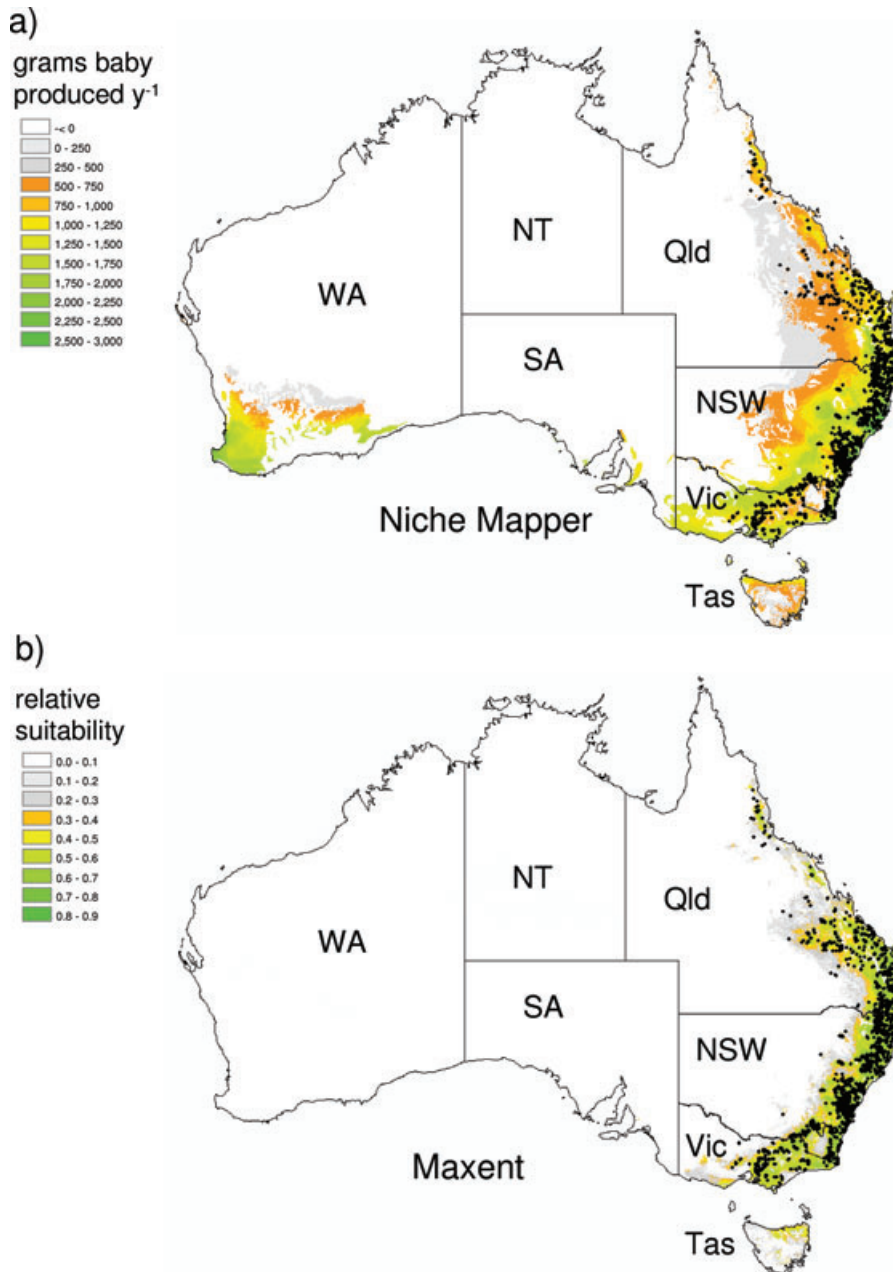


Figure 2 Recent (1990+) observations of the greater glider mapped onto the predicted current distribution of suitable habitat for the greater glider based on (a) Niche Mapper and (b) MaxEnt predictions. Niche Mapper output is the number of grams of offspring produced per annum as limited by

water and energy balance. The Australian states and territories are indicated; Northern Territory (NT), Queensland (Qld), New South Wales (NSW), Victoria (Vic), Tasmania (Tas), South Australia (SA) and Western Australia (WA).

Model comparisons

The mechanistic and correlative models produced similar range predictions (Figure 2), although the similarity was strongest in the northern parts of the species’ range

(Figures 2–4). This is reflected in the correlation between the model outputs. For 99,991 samples randomly scattered across the forested area depicted in Figure 1d, the correlation was modest ($r = 0.477$). However, restricting the comparison to regions north of 29° latitude (i.e., the

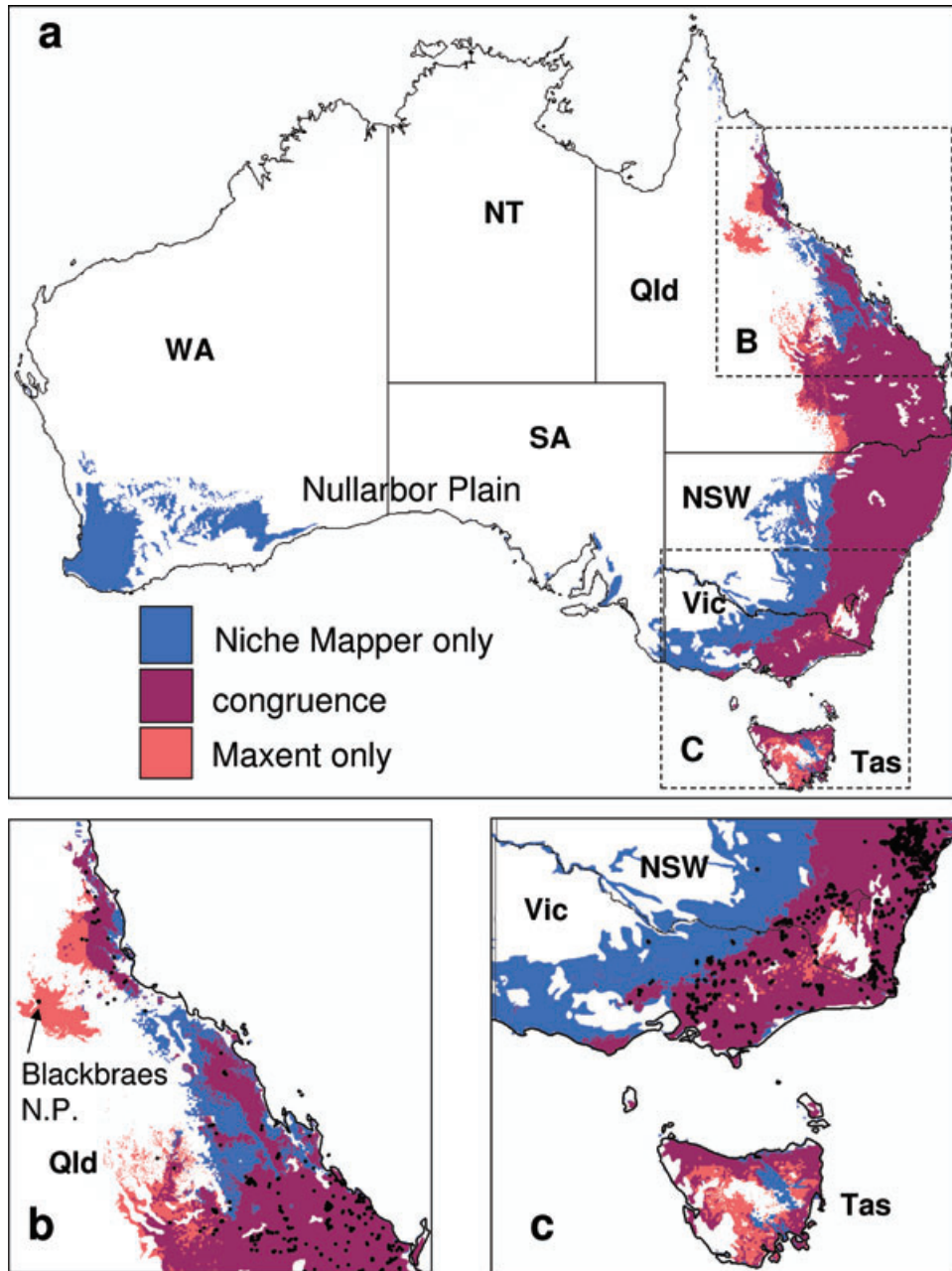


Figure 3 Congruence between the Niche Mapper and Maxent predictions for the whole of the continent (a) and for the northern (b) and southern (c) parts of the range. The current range of the greater glider is also indicated on parts B and C (black dots). The threshold values for Niche Mapper and Maxent are 500g and 0.3, respectively. The Australian states and territo-

ries are indicated; Northern Territory (NT), Queensland (Qld), New South Wales (NSW), Victoria (Vic), Tasmania (Tas), South Australia (SA) and Western Australia (WA). Also indicated is Blackbraes National Park, a site where greater gliders have been observed but which was not included in the development of the Maxent model.

state of Queensland) showed a much tighter relationship ($r = 0.818$). In this region, water was more limiting than energy (Figure 1b).

The degree of congruence between the models can be observed in Figure 3, which shows Niche Mapper gener-

ally to overpredict the range (as expected). In Queensland (Figure 3b), Maxent predicted the range to penetrate farther inland in the far north and captured a point not included in the modeling data set (Blackbraes N. P., Euan Ritchie, James Cook University, pers. comm.).

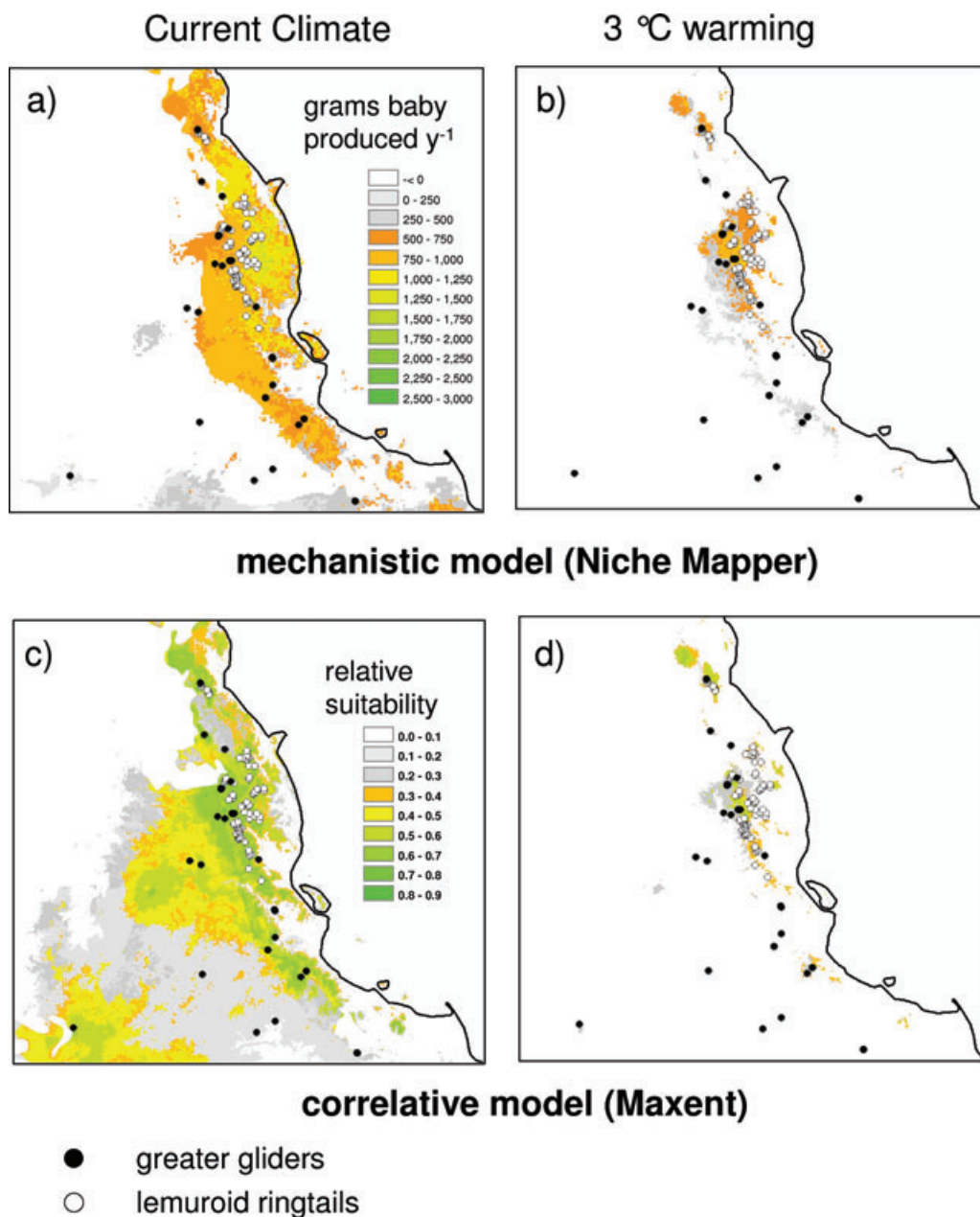


Figure 4 Current and future distribution of suitable environments for the greater glider in the Wet Tropics region of northern Australia as predicted by Niche Mapper (a,b) and Maxent (c,d). Niche Mapper output is the number of grams of offspring produced per annum as limited by water and energy balance. Also indicated is the present known range of the greater glider (black dots) and of its closest relative the lemuroid ringtail (white dots).

Niche Mapper predicted this site as allowing a positive energy balance but with an offspring of 140 g (Figure 4a). In central coastal Queensland, Niche Mapper predicted a wider range than was observed in the greater glider, and than predicted by Maxent (Figure 3b). In Tasmania, Maxent predicted a more southerly potential range than did Niche Mapper (Figure 3c).

Under a uniform 3 °C air temperature rise, all models predicted range contractions in the northern part of the range (Figure 4, Figure S5). While Maxent and Bioclim predicted a greater contraction than did Niche Mapper (94.0%, 98.4%, and 76.3% contraction, respectively), the predictions are similar, indicating almost complete loss of the northern subspecies. In all cases, the remaining

potential habitat corresponds with the current range of a number of similar-sized and closely related folivorous possums restricted to rainforests, including the lemuroid ringtail (Figure 4).

Discussion

We have applied two different approaches to model the distribution and fitness of the greater glider, with qualitatively identical results (Figures 2 and 4). The correspondence between the two approaches is especially striking given that the correlative approach is based on the distribution data, while the mechanistic approach is entirely independent of the distribution data and based instead on fitness arising from interaction between functional traits and environmental conditions.

Model predictions were more strongly in agreement in the north than in the south. The mechanistic model suggests water balance is a constraint in the north (Figure 1b), driven by the costs of evaporative cooling, and this process is also likely to have been captured implicitly by the correlative model via air temperature and rainfall. In much of the south of the range, protein is predicted to be more limiting than energy or water, consistent with physiological expectations for a small-bodied folivore (Foley 1987; Foley *et al.* 1990; Hume 1999). In these areas, distribution and abundance would likely reflect subtle variation in vegetation quality that may be better captured by the correlative model through associations with temperature and rainfall patterns.

Three known greater glider localities in northern Australia are in areas where water (low September rainfall) was predicted to constrain severely the annual production of offspring (Figure 4a). This region was also predicted as marginal by Maxent (Figure 3b). It is possible that gliders in these locations are able to find microhabitats in which local conditions provide sufficient water. Such microhabitats might not be detectable at the 9" resolution of this analysis. The discrepancy of the Niche Mapper and Maxent models in New South Wales and Victoria (Figure 3a,c) might reflect the Maxent model's ability to infer attributes such as site productivity from information on climate and vegetation type.

The two modeling approaches converge to paint a stark picture for northern glider populations. Based on these two independent lines of evidence, if we are unable to mitigate a 3° C warming scenario and we wish to maintain populations of gliders to the north of 25 degrees of latitude, there will need to be a substantial investment in the conservation of climate refugia in which gliders can escape water stress. Protection of sites with high existing glider densities, suitable denning and foraging re-

sources, and which are somewhat buffered against desiccating conditions (i.e., south-facing aspects, sheltered from drying winds) may be important for the long-term persistence of northern greater gliders. Scaling down model predictions to help identify such refugia should be a research priority underpinning a glider conservation program.

Predictions from both of our SDMs might be conservative because they assume that if suitable habitat exists, the species will be able to access and use it. While the predicted suitable habitats appear to be a geographic subset of the currently suitable habitats, actual occupancy and persistence in smaller patches will depend on vegetation dynamics, interspecific interactions, dispersal, and disturbance. A model incorporating these additional processes would likely paint a dire picture for the northern arboreal marsupials. Conversely, however, if there is potential for evolutionary change in these species the impact could be offset (Kearney *et al.* 2009).

The application of correlative SDMs in climate change impact assessment has been criticized (Davis *et al.* 1998; Dormann 2007; Fitzpatrick & Hargrove 2009) because SDMs reflect complex interactions between species that could change as climates change. While the projection of our Maxent model of the greater glider to a 3° C warming involves minimal environmental extrapolation (due to the extent of the survey data), it is uncertain whether the inferred range contraction represents a direct effect of warming on the organism or an interaction with a predator, competitor, or some other ecological process (e.g., fire) that is thermally constrained. However, our Niche Mapper model clearly demonstrates that a substantial part of the Maxent-inferred range contraction probably represents the direct effect of air temperature increases on the water budgets of these mammals. The species simply could not exist in some parts of its current range under a 3° C warming.

A number of similar-sized arboreal folivores, endemic to the Wet Tropics region, including the lemuroid ringtail *Hemibelidus lemuroides*, might already be suffering from climate change (Laurance 2009). These species are likely to respond to temperature rises in a similar manner, and thus our results lend strong support to correlation-only-based predictions of range contraction in these taxa (Williams *et al.* 2003). However, we suggest there have now been sufficient correlative analyses of the potential impact of climate change on species to conclude that climate change represents a serious threat to biodiversity (e.g., Thomas *et al.* 2004; Araújo *et al.* 2006). The challenge now is to prioritize a narrower set of taxa for which more detailed impact assessment should be undertaken and for which climate adaptation strategies should be developed and tested.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Comparison of model predictions of: (a) energy and (b) water use with laboratory data collected in metabolic chambers (Rubsamen 1984). These calculations were based on a 1.14 kg animal assuming an effective wind speed in the chamber of 0.01 m/s and 30% relative humidity. For Figure S1a, triangles and the dotted line represent observed data while closed and open circles represent model predictions using a body length versus width ratio of 3.5 and 4.0, respectively. For Figure S1b, crosses/dotted line represent observed data while circles/solid line represent model predictions.

Figure S2 Model predictions of inner wall temperatures inside heavily shaded, thin-walled cylindrical tree hollows in the Wet Tropics region of northern Australia (17°42' S, 145°32' E) with a greater glider present or absent, in: (a) October and (b) July. Crosses represent shaded air temperature, dotted line represents nest temperature when possum is absent, and solid line represents nest temperature when possum is present during daylight hours.

Figure S3 Logistic predictions of probability of greater glider presence in response to the three strongest environmental variables in the Maxent model. Each response curve is constructed by keeping all other environmental variables at their average sample value and predicting the probability of occupancy under the range of observed predictor variable values.

Figure S4 Continent-wide comparisons of the predicted range of the greater glider as modeled by Bioclim and Maxent under current climate and a scenario of a uniform 3° C air temperature rise.

Figure S5 Current and future distribution of suitable environments for the greater glider in the Wet Tropics region of northern Australia as predicted by Bioclim (a,b) and Maxent (c,d). Also indicated is the present known

range of the greater glider (black dots) and of its closest relative the lemuroid ringtail (white dots).

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