

REVIEW AND SYNTHESIS

Can mechanism inform species' distribution models?

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Abstract

Two major approaches address the need to predict species distributions in response to environmental changes. Correlative models estimate parameters phenomenologically by relating current distributions to environmental conditions. By contrast, mechanistic models incorporate explicit relationships between environmental conditions and organismal performance, estimated independently of current distributions. Mechanistic approaches include models that translate environmental conditions into biologically relevant metrics (e.g. potential duration of activity), models that capture environmental sensitivities of survivorship and fecundity, and models that use energetics to link environmental conditions and demography. We compared how two correlative and three mechanistic models predicted the ranges of two species: a skipper butterfly (*Atalopedes campestris*) and a fence lizard (*Sceloporus undulatus*). Correlative and mechanistic models performed similarly in predicting current distributions, but mechanistic models predicted larger range shifts in response to climate change. Although mechanistic models theoretically should provide more accurate distribution predictions, there is much potential for improving their flexibility and performance.

Keywords

Biophysical model, climate change, climate envelope model, demography, fundamental niche, physiology, realized niche, species' range model.

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INTRODUCTION

Rapid anthropogenic changes in climatic conditions and land use necessitate accurate predictions of how species will respond to environmental changes. Despite this need, fundamental questions persist about how to predict distributions most accurately (Pearson & Dawson 2003; Araujo & Guisan 2006). One primary question is whether a statistical relationship between species localities and environmental conditions is sufficient to predict future distributions (and over what temporal and spatial scales) or whether accurate predictions require a more mechanistic understanding of the processes underlying distributions (Kearney 2006). We address this question by comparing two major approaches for modeling the geographic distributions of species: correlative and mechanistic approaches. Correlative models implicitly incorporate biological processes by statistically estimating environment-range associations from occur-

rences. Mechanistic models explicitly capture hypothetical biological processes and derive their parameters from the phenotypes of organisms, which are then used to construct distributional models. The models differ in their ability to characterize the abiotic, biotic, and historical niches of a species (Soberon 2007), although existing models focus primarily on abiotic constraints.

Correlative models generally require only data on the localities of specimens and their associated environmental conditions. These models have been applied in a wide variety of contexts (Elith *et al.* 2006), such as understanding species invasions (Peterson & Vieglais 2001; Thuiller *et al.* 2005), predicting glacial refugia (Hugall *et al.* 2002; Strasburg *et al.* 2007), delimiting species (Raxworthy *et al.* 2007; Rissler & Apodaca 2007; Stockman & Bond 2007), defining modes of speciation (Graham *et al.* 2004), and identifying conservation hotspots (Rissler *et al.* 2006). A correlative model can accurately predict range dynamics if (1)

constraints on the range omitted by the model, such as correlations between environmental variables, remain constant and (2) the independent variables correspond to the underlying processes that constrain the range (Pearson & Dawson 2003; Dormann 2007). However, the major assumption of correlative models – that processes setting range limits remain fixed in time and space – will likely be violated when making dynamic predictions, such as range shifts during climate change (Williams & Jackson 2007), particularly when extrapolated well beyond current conditions. Despite the likely limitations of correlative models and the theoretical appeal of mechanistic models, we do not know whether mechanistic models can offer more accurate predictions about past, present and future ranges. However, a mechanistic (biophysical) and correlative model were found to differ in their predictions for the distribution of an Australian gecko under past climates, possibly because past climates no longer exist and were thus not incorporated into correlations between contemporary range boundaries and current climates (Strasburg *et al.* 2007).

Mechanistic models differ from correlative models because they rely on our understanding of the dominant processes that underlie survival and reproduction to predict a geographic range (Helmuth *et al.* 2005; Kearney & Porter 2009). For this reason, the ideal mechanistic model (i.e. one that describes all important processes potentially constraining a species' range) should better predict range dynamics than would a correlative model. However, mechanistic models require an accurate understanding of a species' fitness relationships with the environment and estimates of many phenotypic parameters under a wide range of environmental conditions (Table 1). Errors in parameters can compound leading to poor accuracy in prediction. In addition, these models are typically tailored to certain species, and thus require substantial revision before they can be applied to new species.

Presently, the relative advantages and disadvantages of correlative and mechanistic models are largely speculative. To date, the few comparisons of the abilities of correlative and mechanistic models to predict observed distributions have examined only a single mechanistic model. These

comparisons have been focused on another issues (Buckley 2008 on geographic trait variation; Morin & Thuiller 2009 on future predictions) or only included a qualitative comparison (Kearney & Porter 2009; Strasburg *et al.* 2007). Hijmans and Graham (2006) compared several correlative models to the predictions of a mechanistic plant growth model (treated as the true distribution). Detailed comparisons between and among correlative and mechanistic models can provide insights about the constraints on species' ranges as well as assess the models' predictive capacities.

Here, we compare four approaches to modeling species' ranges that span the correlative and mechanistic spectrum. Specifically we address two basic questions. First, how do range predictions based on phenomenology and those based on mechanism differ? Second, how simple can we make a mechanistic model and still generate useful predictions? We address these questions by comparing the performances of correlative models to three types of mechanistic models under current climate conditions and a uniform warming of 3 °C, which represents a moderate scenario for the next century (Solomon *et al.* 2007). Specifically, we compare the ability of these models to predict the ranges of two focal organisms: the sagem skipper (*Atalopedes campestris* Boisduval 1852) and the eastern fence lizard (traditionally *Sceloporus undulatus* Bosc and Daudin 1801, but see below). These organisms were chosen because their use in previous theoretical and empirical studies enabled us to parameterize the mechanistic models (see Crozier & Dwyer 2006; Buckley 2008). We note that populations of eastern fence lizards, *Sceloporus undulatus*, were recently divided into four major lineages, which have each been proposed as evolutionary species (Leache & Reeder 2002; Wiens *et al.* 2010). Although we parameterized our models using primarily data for one of these lineages, we apply this prediction to all four lineages to be consistent with previous modeling exercises (Buckley 2008). In our Discussion, we address the potential errors resulting from our application of the models to a clade with geographic variation in the phenotype. For simplicity, we refer to these four lineages of the species group as *Sceloporus undulatus* (*sensu lato*). We reran correlative models including specimen localities for species parapatric

Table 1 The biotic and abiotic data required for parameterizing five classes of range models and the current and potential model components [demography, biotic constraints (species interaction and movement limitations), and evolution]

Model	Data requirements		Components and extendibility		
	Biotic	Abiotic	Demography	Biotic constraints	Evolution
Correlative	Localities	Data layers		Implicit	Updating
Biophysical threshold	Traits, thresholds	Heat flux variables			Traits
Life history	Demography	Data layers	✓	Possible	Curves
Foraging energetic	Traits	Heat flux variables	✓	Possible	Traits

with *S. undulatus* (*S. cautus*, *S. belli* and *S. woodi*, Leache & Reeder 2002) to confirm that omitting these localities did not alter model predictions.

We used multiple approaches for correlative and mechanistic modeling. For the correlative models, we used two statistical algorithms to relate locality data to bioclimatic variables describing temperature and precipitation. For the mechanistic models, we used three approaches that vary in their degree of complexity and the specific way that traits are linked to range limits. The first mechanistic model that we explore computes an environmental threshold for persistence based on an organism's physiology. This model computes the energy budget of an organism with a specified set of traits (e.g. size, critical thermal limits, solar reflectivity) under particular environmental conditions (Bakken 1992; Porter *et al.* 2000, 2002). The model produces spatially explicit maps of ecologically relevant parameters, such as the potential duration of activity or the food required to meet energetic costs. To predict a range limit, however, one must assume an environmental threshold, such as time required for development. This threshold represents a hard limit (*biophysical threshold*) that only partially correlates with demography (Kearney & Porter 2004). If the model is accurate, then it should accurately predict that occupied sites are within these hard limits. The other two mechanistic models predict the range by explicitly computing population dynamics. The *life history* model uses empirical relationships between environmental temperature and organismal performances to characterize fitness across a range of specified environment (Crozier & Dwyer 2006). The *foraging energetic* model uses optimal foraging theory to link individual energetics to population dynamics (Buckley & Roughgarden 2005; Buckley 2008). We quantitatively compare these models and discuss reasons for differences in model predictions.

METHODS

Environmental and distributional data

Throughout our comparison, we standardized the origin and resolution of data. We used average monthly values of air temperature, variation in daytime air temperature, soil temperature, wind speed, relative humidity, elevation and albedo (1961–1990 with 10' resolution, New *et al.* 2002) for an equal-area projection and equal-area grid cells (343 km²) equivalent to 10 min near the equator. We restricted our analysis to the United States (despite the presence of both species in Mexico) due to data availability. For the correlative models, we initially used variables describing temperature, diurnal temperature range, precipitation, wind speed and humidity to derive variables analogous to the WorldClim climate data commonly used in correlative models (<http://www.worldclim.org>, 1960–1990, Hijmans

et al. 2005). The correlative models were subsequently implemented with only the temperature variables (maxent temp and GLM temp), to ensure comparability with the prime drivers of the mechanistic models. For the biophysical and foraging energetic models, we used the data to model hourly temperatures using a sine approximation. The use of temperature and wind speed at the standard weather station height of 2 m may underestimate the temperatures experienced by lizards close to the ground. Indeed, model predictions are quite sensitive to our choice of environmental data (Figure S1 and Appendix S1). We note that the use of monthly data eliminated a potential advantage of the mechanistic model – the ability to include stochastic, daily variation; this variation seems crucial to accurately modeling important events that lead to mortality or reproductive failure (Helmuth *et al.* 2002, 2005). However, using more finely resolved climatic data in the correlative models would be impractical and we wanted to maintain data comparability between the modeling approaches (potentially at the expense of some mechanistic model performance). We assembled locality data and a range map for each species (Appendix S1). Range maps typically use large polygons to describe the outer edges of a species range. This limits our ability to assess the models' performance in describing patchiness within the range.

Correlative models

We used Maximum Entropy (maxent) and Generalized Linear Models (GLM) to correlate species' localities and climate data. Distributions were modeled using the MAXENT software, version 3.2.1 (Phillips *et al.* 2006), which derives the distribution maximizing information entropy subject to constraints set by the association between the presence points and the environmental variables (Phillips *et al.* 2004). Logistic regression in Matlab was also used to relate the bioclimatic data and species' localities. In this approach, we found the reduced set of bioclimatic variables in the logistic model that minimized the Akaike Information Criterion (AIC) by applying an iterative process of removing variables from the full model until no further improvements in AIC occurred (Burnham & Anderson 2002). Logistic regression could not be used for *S. undulatus* because absences were unavailable. In such cases, absence-dependent methods sometimes are applied after inclusion of pseudo-absences. However, more commonly, presence-only techniques are applied. We took this approach and only applied maxent to the data for *S. undulatus*. We standardized the thresholds of occurrence probability used to predict range limits to 10% for maxent models (Stockman & Bond 2007) and 50% for GLM models (Liu *et al.* 2005), which are the thresholds most commonly used. While more sophisticated statistical algorithms for choosing a threshold can improve predictive

ability (Liu *et al.* 2005), we use a fixed-threshold because it is the most common implemented method.

Mechanistic models

Biophysical threshold models

Biophysical models are often invoked to calculate operative environmental temperatures (T_e , the steady-state temperature of an animal with specified thermal and radiative properties in a given environment). Operative environmental temperatures are calculated by adjusting air temperature for absorbed radiation, wind speed, and animal morphology (Bakken *et al.* 1985; Campbell & Norman 2000). The duration of foraging at any given location can be assessed by examining whether T_e s falls within an observed range of field-body temperatures. This duration provides a basis for modeling potential energy gain and population dynamics in the foraging energetic model; the duration of foraging can be used directly to predict range limits if a biological threshold is determined *a priori* (e.g. annual foraging duration required for development).

For *S. undulatus*, we used the modeling approach of Campbell & Norman (2000) as implemented in Buckley (2008). The approach is similar to, but less detailed than, the ecophysiological models of Porter and colleagues (Porter *et al.* 2000, 2002, 2006; Kearney & Porter 2004). Lizards were considered active when operative temperatures (calculated for full sun and full shade, where observed radiation equals zero) overlapped the observed range of field body temperatures for activity. To link this biophysical model to a geographic range boundary, we calculated *a priori* the time required for a female to procure sufficient energy for reproduction. First, we estimated maximal surplus energy by subtracting the field metabolic rate (estimated as twice the resting metabolic rate, or $10.8 \text{ J g}^{-1} \text{ h}^{-1}$) from the metabolizable energy intake ($16.4 \text{ J g}^{-1} \text{ h}^{-1}$) at the mean preferred body temperature of $33 \text{ }^\circ\text{C}$ (Angilletta 2001a,b). We then multiplied the mean annual egg production of *S. undulatus* (22.5 eggs) and the energetic content of individual eggs (3268 J) to calculate annual energetic requirements. Given this requirement, we determined the minimal duration of foraging at the assumed rate of energy gain that was required to produce eggs (1315 h). This criterion assumes that, on average, populations of *S. undulatus* remain constant in size, such that a female must produce 22.5 eggs to offset the expected mortality.

We used a biophysical threshold to predict a range limit for *A. campestris* by predicting *a priori* the degree days required for embryonic or larval development. Degree days accumulated incrementally for each $1 \text{ }^\circ\text{C}$ that mean temperature on a given day exceeded the minimal developmental threshold ($15.5 \text{ }^\circ\text{C}$, data: <http://www.ncdc.noaa.gov>). We chose the mean degree days required for the completion

of two generations (834 degree days, Crozier & Dwyer 2006) as the threshold for determining the range limit. Two generations per year is the minimum observed in natural populations (Crozier & Dwyer 2006).

Life history models

Life history models use empirical estimates of survivorship and fecundity to model the annual per capita rate of population growth (λ) as a function of temperature, T . The range of a species is defined as those areas in which populations are self-sustaining (i.e. $\lambda \geq 1$). The model for *A. campestris* is detailed in Crozier & Dwyer (2006). Briefly, Crozier & Dwyer (2006) split the life cycle into winter survivorship, $\Phi(T)$, and net summer recruitment, $R(T)$, where $\lambda = \Phi(T)R(T)$ (Appendix S1). Winter survivorship was fitted to empirical data as a logistic function of temperature; census data were used to estimate reproductive rates; and field experiments were used to develop a relationship between the number of summer generations and the degree days available for development. We then used maps of degree days to generate location-specific estimates of net summer recruitment.

We implemented an analogous model to calculate λ for *S. undulatus*, except that we did not separate winter and summer survivorship [i.e. $\lambda = R(T) = R_0(T)$] because these data do not exist. The model was derived from demographic data from field populations across the U.S. (Angilletta *et al.* 2004, 2006; Niewiarowski *et al.* 2004). Specifically, we assumed the following: lizards mature at 1 or 2 years of age depending on environmental temperature (see Angilletta *et al.* 2004); annual survivorships of juveniles and adults remain constant over time but vary with temperature; and annual fecundity remains constant throughout life but varies with temperature. Given these assumptions, the per capita net recruitment is

$$R_0 = \sum_{x=\alpha}^L s_j(T)^{\alpha(T)} s_a(T)^{x-\alpha} m(T),$$

where T is mean annual temperature, α is age at maturity (years, $\alpha = 1$ if $T > 15 \text{ }^\circ\text{C}$ and $\alpha = 2$ otherwise), s_j is the annual probability of juvenile survival ($s_j = 0.324T - 0.012$), s_a is the annual probability of adult survival ($s_a = -0.029T + 0.728$), m is the annual fecundity ($m = -0.391T^2 + 12.560T - 73.038$), and L is the maximal lifespan in years. We assumed $L = 4$, but the range prediction was invariant within the biologically reasonable range of 3–5 years. The range prediction was also invariant to thermal effects on age at maturity because the earlier maturation associated with increased temperature is cancelled by a higher mortality rate (potentially due to longer exposure to predators during activity; Angilletta *et al.* 2004). Consequently, the probability of surviving to maturity is nearly independent of temperature and can be assumed to be constant, $s_j^z = 0.089$.

Foraging energetic models

Rather than empirically estimating recruitment, the next set of models derives recruitment rates from the energetic yield of foraging. The population dynamic models were based on a biophysical model that estimated the potential duration of foraging (Appendix S1). We modeled the net energetic yield from this foraging and translated this energy into offspring to estimate recruitment. The model for *S. undulatus* is detailed in Buckley (2008). Energetic yield was calculated using an optimal foraging model for a territorial central place forager (which is an appropriate behavioral assumption for this lizard). The model incorporates empirical estimates of metabolic rates, lizard running speed, prey density, and density-dependence via a restricted foraging range. Population dynamics were modeled using empirical estimates of the energetic cost of producing an egg and mortality rates.

For *A. campestris*, we developed a model analogous to the life-history model for *S. undulatus*, but we estimated R_0 based on foraging energetics, $R_0 = bE - \gamma$, where the energetic yield of foraging E (J s^{-1}) was estimated from empirical data. Here, b is the reproductive rate per unit of net energetic yield and γ discounts egg production by metabolic costs during inactivity. Energetic yield was calculated as a function of foraging time (Appendix S1). We used the average of resting metabolic rates (e_w) for the gulf fritillary, *Agraulis vanillae*, and the cloudless sulfur, *Phoebis sennae* ($e_w = 0.0019 \text{ J s}^{-1}$) (May 1992) because rates for *A. campestris* have not been measured. Rates of net foraging profitability (E) were averaged between these two butterfly species and among eleven nectar plants species ($E = 0.29 \text{ J s}^{-1}$) (May 1992). We estimated m as the product of the quantity of eggs produced per joule for *Euploea core* ($0.0081 \text{ eggs J}^{-1}$, Hill 1989) and the seasonal (summer) probability of surviving to adulthood (12%, Crozier 2004). We examined the sensitivity of the model predictions to the four parameters derived from other species (e_w , E , m and net foraging rate). Halving or doubling the values of each parameter (data on parameter ranges was not available) contracted or expanded the range predictions by less than 1%. The model is not sensitive to these parameters because the differences in energy input and use resulting from varying each parameter has a small influence on the model relative to differences in activity time. We assumed a 10-day life span for adults. We further assumed that 10% of potential activity time was allocated to foraging and 50% was allocated to searching for oviposition sites. These assumptions represent free parameters that did not qualitatively influence our predictions. We additionally used empirical relationships to include the thermal dependence of egg maturation and ovipositing and density dependence for nectar in the model (Appendix S1).

Comparison of models

We relied on two indices to compare model predictions to grid cell presences (corresponding to the range polygon): the sensitivity index (%+) is the proportion of true presences correctly predicted (true presences predicted divided by the total number of true presences, Manel *et al.* 2001). The specificity index (%-) is the proportion of true absences correctly predicted (true absences predicted divided by the total number of true absences, Manel *et al.* 2001). Model performance (% true) combines the first two metrics by calculating the percentage of all cases that are correctly predicted (true presences plus true absences divided by total cases, Manel *et al.* 2001). We also examined the percent of specimen localities and survey data correctly predicted. For ranges predicted following climate change, we examined the expansion, contraction, and maintenance of range area as a proportion of initial range area. We also compared the predicted range area before and after climate change.

RESULTS

Sceloporus undulatus

The most striking difference among the predictions for *S. undulatus* was that the correlative model more closely predicted the western limit of this species, whereas the mechanistic models predicted that thermally suitable habitat was available throughout the southern United States (Figs 1 and 3a and Figure S1). The prediction of the western range boundary in the maxent model is partially, but not entirely, due to the inclusion of precipitation (as indicated by comparison with the maxent model with temperature only). While the northern limit was predicted reasonably well by the correlative, life-history, and foraging energetic models, the biophysical threshold model severely underpredicted this boundary. The proportion of grid absences and presences as well as localities correctly predicted (% true) by the maxent model was somewhat higher than those for the other models (Table 2). The maxent model with only temperature exhibited weaker performance than the life history and foraging energetic model.

The predicted shift in the range of *S. undulatus* in response to a uniform warming of 3 °C varies among models (Figs 1 and 3b). The ratios of range area after warming to the range area before warming predicted by the mechanistic models (biophysical threshold model: 4.09, life history: 1.40, foraging energetic: 1.55) exceed those predicted by the correlative models (maxent: 1.10, maxent temp: 1.00). Analogously, the range expansion predicted by the mechanistic models were more substantial (life history: 51%, foraging energetic: 55%) than those predicted by the correlative models (maxent: 14%, maxent temp:

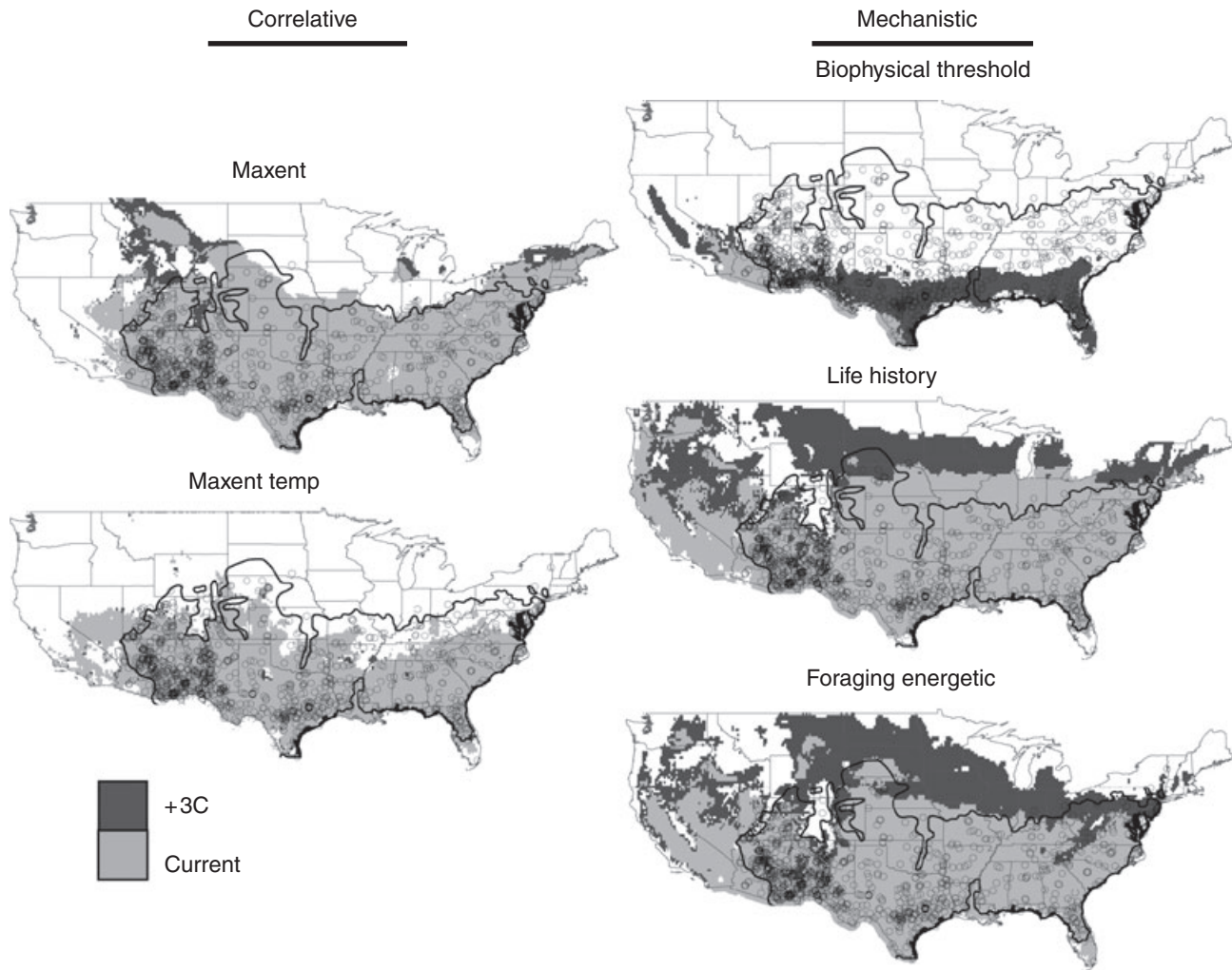


Figure 1 Range predictions for *Sceloporus undulatus* in current climates (light gray) and predicted range expansions following a uniform 3 °C temperature increase (dark gray). Localities (o) and the atlas range polygon are shown.

Table 2 We compare range predictions to atlas range polygons and county occurrences using the sensitivity index (%+), the specificity index (%-), and the model performance (% true). We also report the percent of specimen localities (% localities) and survey data (presences: % survey + and absences: % survey -) correctly predicted

Model	<i>S. undulatus</i>				<i>A. campestris</i>				
	%+	%-	% true	% localities	%+	%-	% true	% survey +	% survey -
Correlative-maxent	0.97	0.76	0.85	0.99	0.80	0.75	0.78	0.98	0.46
Correlative-maxent temp	0.42	0.86	0.67	0.41	0.51	0.93	0.73	0.85	0.69
Correlative-GLM					0.64	0.89	0.78	0.73	0.81
Correlative-GLM temp					0.66	0.91	0.80	0.68	0.82
Biophysical threshold	0.04	0.95	0.57	0.04	0.67	0.85	0.77	0.81	0.70
Life history	0.82	0.66	0.73	0.84	0.60	0.90	0.76	0.79	0.69
Foraging energetic	0.84	0.71	0.76	0.84	0.85	0.44	0.63	0.91	0.40

6%). The biophysical threshold model, which underpredicted the current range, predicted a range expansion of 309% following climate change. Only the life-history and

maxent models predicted range contractions at the southern limit (11% and 4%, respectively). The maxent model based on temperature alone predicted no net change

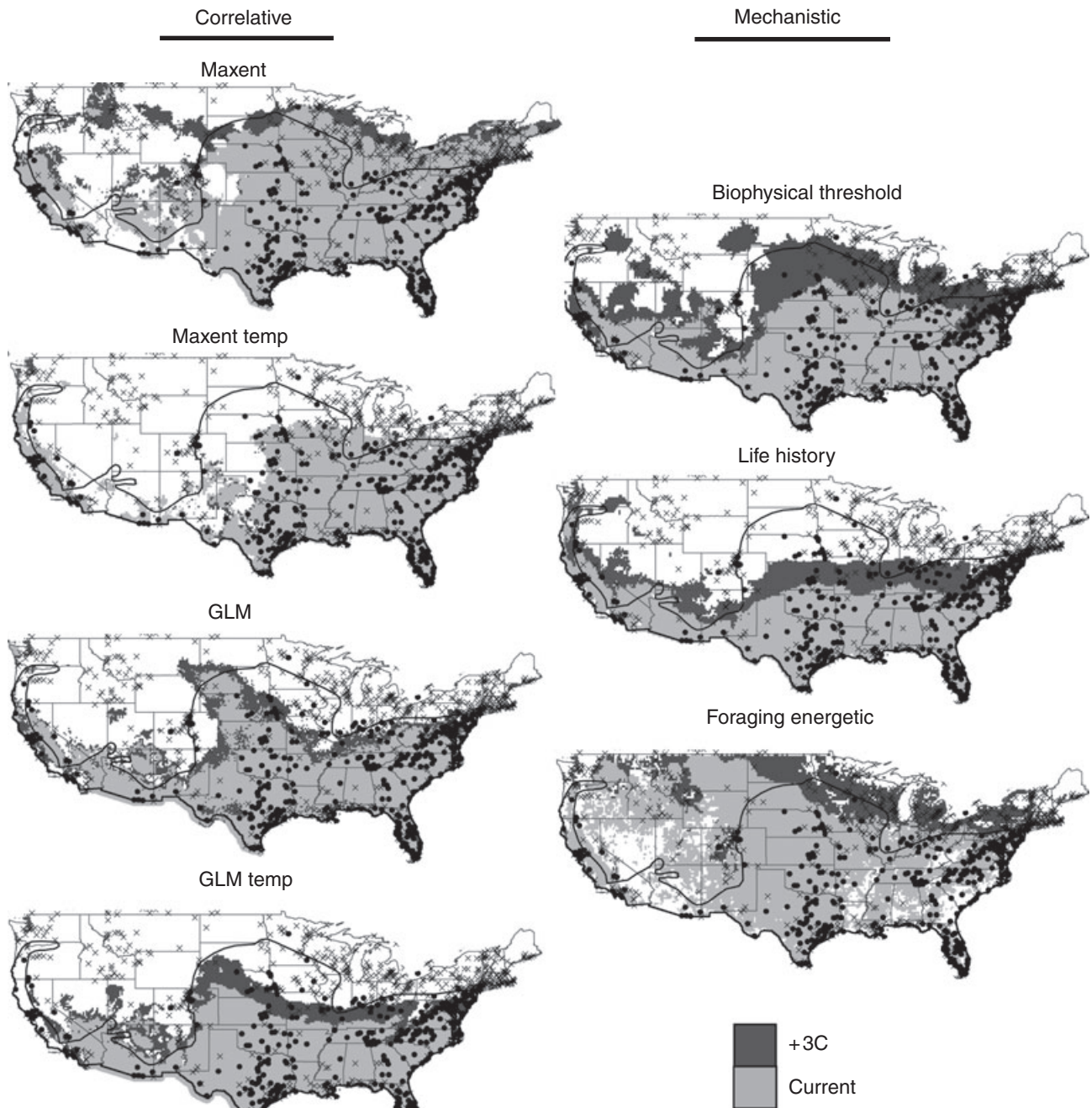


Figure 2 Range predictions for *Atalopedes campestris* in current climates (light gray) and predicted range expansions following a uniform 3 °C temperature increase (dark gray). Presences (o) and absences (x) from the 4th of July butterfly count are indicated along with the atlas range polygon.

in the range following a 3 °C warming, due to a 6% range expansion balanced by a 6% range contraction.

Atalopedes campestris

All models predicted qualitatively similar ranges for *A. campestris*, but the foraging energetic model overpredicted

the range more than the other models (Figs 2 and 3a and Figure S2). This overprediction suggests that we mischaracterized the ability of this species to acquire sufficient resources for persistence or that something other than resource acquisition limits the range. The life-history model imposed an additional constraint related to winter temperature beyond the developmental time constraint reflected in

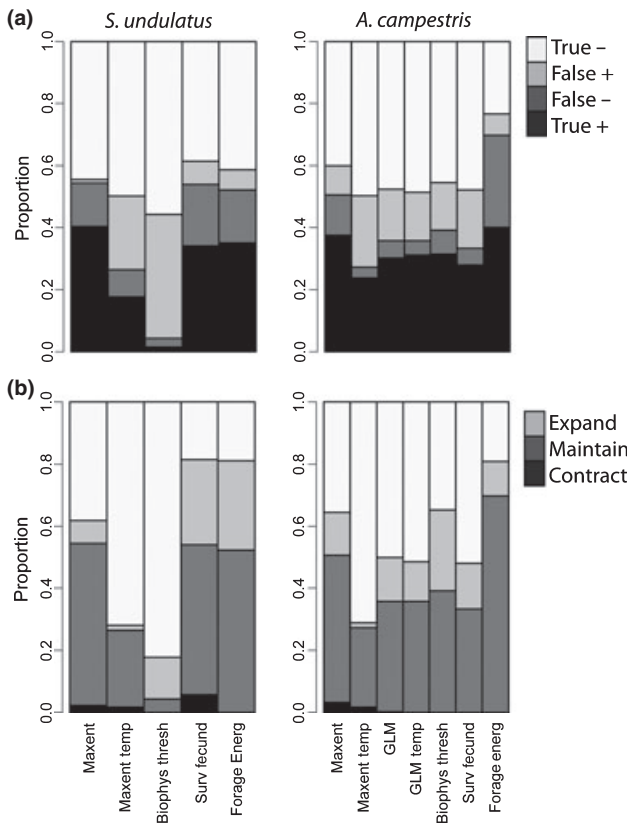


Figure 3 A comparison of range models for *Sceloporus undulatus* and *Atalopedes campestris*. We depict (a) the proportion of grid cells that with true predicted presences, false absences, false presences, and true absences generated by comparing the model predictions with the range polygon and county localities and (b) the proportional range expansion, contraction, and maintenance in response to a uniform 3 °C temperature increase varies between models.

the biophysical threshold model. The inclusion of a winter-survival constraint contracted the range prediction and leads to under-prediction in cold regions. The biophysical and life-history models excluded the recently colonized part of the range in the state of Washington. The maxent model slightly overpredicted the northern range edge, whereas the GLM model underpredicted certain portions. All models performed similarly in quantitative metrics (73–80% predictive success), with the exception of the foraging energetic model (63% predictive success).

The range shifts predicted by mechanistic models for *A. campestris* following a 3 °C warming were more consistent than those predicted for *S. undulatus* (Figs 2 and 3b). The ratio of predicted range area following a 3 °C warming to initially predicted range area varied among models (maxent: 1.21, maxent temp: 1.00, GLM: 1.39, GLM temp: 1.36, biophysical threshold model: 1.67, life history: 1.44, foraging energetic: 1.16). The correlative models predicted smaller

range expansions (maxent: 27%, maxent temp: 6%, GLM: 39%, GLM temp: 36%) than did the biophysical threshold and life-history models (67% and 44%, respectively). The difference between the predictions of these mechanistic models suggests that developmental time will respond more strongly to warming than will winter survivorship. Range expansion in the foraging energetic model may be constrained by resource availability (estimated by landcover, 16%), which may be altered by climate change. Only the correlative models predicted slight range contractions at the southern limit (maxent: 6%, maxent temp: 6%, GLM: 1%, GLM temp: 0%). As was the case with *S. undulatus*, the maxent model based on temperature alone predicted no net range change following a 3 °C warming due to a 6% range expansion in the north balanced by a 6% range contraction in the south. For both species, the maxent model based on temperature alone predicted a more restricted range than the maxent model with additional environmental variables.

DISCUSSION

Challenges in mechanistic modeling

In the most extensive comparison of correlative and mechanistic models to date, we found that the correlative and mechanistic models performed similarly when predicting contemporary ranges. In some cases, the mechanistic models generated poor predictions, potentially revealing important insights into model development. Mechanistic models might fail to predict a species' current range for two reasons.

First, a mechanistic model focuses on particular constraints, but these constraints (and those identified by correlative models) might not be the most important ones in all areas of a species' range. In addition, because current mechanistic models focus on a limited set of abiotic constraints (primarily thermal constraints), the interaction between different abiotic constraints and those between abiotic and biotic constraints could cause observed ranges to deviate from predicted ranges. Our mechanistic models focused entirely on thermal constraints; therefore, we expected them to over-predict the range, especially where we think biotic factors also limit distributions. Consistent with this prediction, the sensitivity index (%+, correct prediction of presence) exceeded the specificity index (%–, correct prediction of absence) for the life-history and foraging energetic models of *S. undulatus*' range (Table 2). Furthermore, correlative models based on both temperature and precipitation overpredicted the range of *S. undulatus* in the western U.S. This overprediction may reflect a biotic constraint resulting from interactions with other lizards in the *Sceloporus undulatus* species group. Indeed, the regions of overprediction are currently occupied by species that are

closely related to the populations traditionally designated as *Sceloporus undulatus* (Leache & Reeder 2002; Wiens *et al.* 2010). Given that these members of the *S. undulatus* species group share similar behaviors, physiologies, and morphologies, we were not surprised to learn that the mechanistic models predicted the occurrence of lizards beyond the range observed for the clade that we considered (i.e. the four major lineages traditionally classified at *S. undulatus*). Moreover, we would have overpredicted the range of *S. undulatus* far more had we considered only the lineage that was recently designated at *S. undulatus (sensu stricto)* and ignored the three other lineages that were traditionally included in *S. undulatus* (now classified as *S. cowlesi*, *S. consobrinus*, and *S. tristichus*; Wiens *et al.* 2010). Thus, our analyses for fence lizards illustrates how a comparison of mechanistic and correlative models helps to distinguish a species' realized and fundamental niches (Kearney 2006) and provide predictions that can be tested by experimentation. Also, correlative models, when used in conjunction with mechanistic models, can suggest particular traits or processes to include in a mechanistic model. For example, the correlative models suggest that including precipitation can improve model performance.

Second, mechanistic models can perform poorly when parameters are estimated with error. Parameters such as the minimal activity time for population persistence have not been measured reliably in the field yet have a strong effect on the predicted range. Error in key parameters likely explains our under-prediction of the range in some regions, because mechanistic models make predictions based on estimates of the minimal conditions necessary for survival and growth. For example, we note that grid cell means are unlikely to capture the range of temperatures available in any given location. Our biophysical model for *S. undulatus* likely underestimated the operative temperatures experienced by lizards due to using air temperatures recorded at a height above lizards (Figure S1). Furthermore, our use of monthly data might have limited the predictive power of the mechanistic models. In this species group (Leache and Reeder 2002), unique phenotypes may behave in significantly different ways, creating error when modeling the entire range from the mean phenotype. However, few studies have explicitly incorporated geographic variation in traits or genetic variation across a range in mechanistic models (but see Buckley 2008; Morin & Thuiller 2009). Thus more integration between evolutionary biologists and ecologists is needed to improve our predictions of species ranges.

Extrapolating range models

Mechanistic models exhibited similar or weaker performance in predicting current distributions relative to

correlative models, despite the extra effort and additional data required for their implementation. However, mechanistic models do address two major criticisms that have been levied against correlative models. First, statistical models predict the probability that a species occupies a grid rather than a rate of population growth (but see Keith *et al.* 2008, which incorporates stochastic population dynamics), making it difficult to define the threshold probability that should delimit the range (Phillips & Dudik 2008; Warren *et al.* 2008). Second, correlations might not reflect the mechanisms underlying a species' distribution (Olden & Jackson 2000; Meynard & Quinn 2007). This misrepresentation can result from overfitting models to error in the original data (Olden & Jackson 2000; Burnham & Anderson 2002; Elith *et al.* 2006; Randin *et al.* 2006) or failing to represent complex non-additive relationships with environmental variables (Araujo & Guisan 2006; Meynard & Quinn 2007). The ability of the model to predict an existing range does not necessarily reflect its ability to predict the future range, especially when the environment changes or the range is not at equilibrium (Thuiller 2004; Urban *et al.* 2007). Species from the same region have shifted to different extents and in different directions during paleological changes in climate (Davis 1981; Graham *et al.* 1996; Jackson & Overpeck 2000; Wing *et al.* 2005), suggesting that a standard correlative model would have failed to predict these distributions (reviewed in Williams & Jackson 2007).

The ability of correlative and mechanistic models to predict current distributions is broadly similar in our comparison. However, the mechanistic models tended to exhibit more pronounced responses to a uniform warming of 3 °C. The reasons for this difference remain uncertain but could relate to how these models predict species ranges. Specifically, mechanistic models tend to aggregate responses over time whereas correlative models assess responses based on temporal averages. For example, if climate change increases activity time in a specified location, the increased activity time will sum across hours in a biophysical threshold model. However, a recent comparison of a mechanistic model based on physiological probabilities and an ensemble correlative model (Morin & Thuiller 2009) suggested that correlative models predict greater climate responses for plants than mechanistic models; in this case their mechanistic model may be less sensitive to climate change due to its inclusion of phenotypic plasticity and local adaptation. Our comparison suggests that forecasting or hindcasting distribution models will be essential to assess which class of models yields more realistic predictions of range dynamics (Randin *et al.* 2006). Unfortunately, we lack sufficient knowledge of the historical distributions of most species, and particularly our focal species, to hindcast their distributions. Previous

efforts to hindcast ranges with multiple correlative models have revealed mixed success in predicting range dynamics (Araujo *et al.* 2005; Randin *et al.* 2006). Mechanistic models have succeeded in hindcasting thermal stresses consistent with past range changes (Jones *et al.* 2009; Wethey and Woodin 2008).

Selecting and improving range models

In light of the similar performances of the models considered here, we suggest that the intended application should inform the choice of a modeling approach. To predict the current distribution of a well-sampled species with a distribution in equilibrium, correlative models should provide both expediency and performance. If a species is known to be constrained by a particular physiological condition, a biological threshold model would be a solid choice requiring only information about morphological and physiological traits. However, as our comparison demonstrates, an inappropriate threshold or microclimate characterization can lead to erroneous predictions even for well-studied species. The choice of life-history and foraging energetic models may be restricted to those cases where demographic constraints aggregated over time crucially determine the range. Demographic models are more difficult to implement, but offer increased flexibility and extensibility that might be needed when predicting distributions in novel environments (Table 1). The detailed empirical studies required to implement the life-history models can be prohibitive. The emphasis on species' traits in the foraging energetic model can facilitate parameterization and minimize the assumptions required to predict range dynamics. However, using parameter values from related species will often be required (as was done here for *A. campestris*), and this approach can introduce error.

Mechanistic models might also be preferred if complex spatial and temporal patterns of thermal stress (e.g. biophysical mechanistic models) are central to constraining distributions; these are averaged in correlative models and even in some broad-scale mechanistic models (Helmuth *et al.* 2002, 2005). Applying mechanistic models to marine systems has enabled addressing multiple aspects of thermal stress that can be used to predict distributions (Wethey & Woodin 2008; Jones *et al.* 2009). Mechanistic models might also be preferred when phenotypes vary across the range because the range implications of this variation can be directly addressed using mechanistic models (Buckley 2008; Kearney & Porter 2009). However, correlative models can indirectly address phenotypic variation by modeling lineages rather than species (Peterson & Holt 2003; Rissler *et al.* 2006). In fact, improving both correlative and mechanistic models will require greater information on geographic variation in traits (phenotypic and genotypic) across a range.

Our comparison highlights three avenues for improving mechanistic models (and some of these suggestions can also be applied to correlative models). First, we need to develop mechanistic models that are sufficiently general to enable application to a variety of species while remaining feasible to parameterize. Crucial to this goal is collecting the behavioral and physiological data needed to parameterize these models. This effort will require intensive studies of focal species in the laboratory and field. These models should explicitly predict population growth, rather than organismal performance, to maintain a tight link with absolute fitness and to limit the arbitrary nature of performance thresholds that we encountered with our biophysical model.

Second, the sensitivity of the models to parameter uncertainty should be analyzed to prioritize further data collection and to clarify the proportion of the total error that might be accounted for by this source. Sensitivity analyses for the *A. campestris* life-history (Crozier & Dwyer 2006) and foraging energetic models and the *S. undulatus* foraging energetic (Buckley 2008) model reveal that changes in the value of individual parameters (other than threshold values) are unlikely to qualitatively influence our model comparison. Taking the example of a bioenergetic model for *S. undulatus*, sensitivity analysis found that the range predictions were relatively robust to altering insect abundance by 50% (Buckley 2008). While prey availability is important, the sensitivity analysis suggests that collecting empirical data on thermal traits is a higher priority than data on prey availability. We have not included sensitivity analyses for the other models used here as these models are less amenable to such analyses. However, a similar approach can be achieved using the correlative approach by examining the effects of systematically excluding independent variables or by adding noise that changes the correlation structure among independent variables. Here, the evaluation of mechanisms is less clear, but this approach still might help reveal important processes that determine species' ranges (as revealed by our correlative predictions based strictly on temperature). Regardless, such sensitivity analyses will better inform researchers who adopt either mechanistic or correlative approaches.

Third, we can improve both mechanistic and correlative models by including a range of important, but often neglected, mechanisms. Generally, extending a mechanistic model is more straightforward because it explicitly describes demographic processes. One important extension to mechanistic models would be to include biotic interactions because these interactions can constrain a species' range substantially (Davis *et al.* 1998; Pulliam 2000; Heikkinen *et al.* 2007). Species' interactions constrain the localities used to parameterize correlative models. This can be problematic as species' interactions often change during climate change (Dormann 2007; Williams & Jackson 2007). Correlative

models including data on other species distributions can explicitly address these biotic constraints (Araujo & Luoto 2007), but their performance will be affected by changes in communities. Including evolutionary dynamics is another important initiative (Kearney & Porter 2009). Range models based on organismal traits can be modified to accommodate a variety of existing theories about adaptation to changing environments (Lynch & Lande 1993; Gilchrist 1995). Likewise, life-history models could be used to predict the range implications of evolution by enabling the evolution of performance curves, which depict the relationship between an environmental variable and fitness (Huey & Kingsolver 1993). Finally, movement rates could be added to models to allow for a lag between environmental change and the species ability to track this change (Guisan & Thuiller 2005). This factor might be especially important for poor dispersers, but might not be necessary for good dispersers (Crozier & Dwyer 2006).

Besides improving mechanistic models *per se*, we could also combine mechanistic and correlative approaches. This integrated approach provides a promising middle ground that could enable sound and practical predictions of range dynamics in changing environments. Given the large amounts of time and effort required to parameterize mechanistic models, correlative models will continue to provide much-needed predictions about species for which we currently lack mechanistic data (Guisan & Thuiller 2005). In the end, we see value in a dynamic interplay between mechanistic and correlative modeling approaches. Environmental factors found to increase the accuracy of correlative models might suggest additional processes to add to a mechanistic model. These elusive signals embedded in correlative models can then inform mechanistic approaches which will help elucidate the biological constraints on species' ranges. A viable hybrid approach would include the output of a mechanistic model, such as potential activity times and growth rates, in a correlative model that includes other factors that likely play a role but their mechanistic relationships with environmental variation have not yet been described or parameterized. Assuming the underlying mechanism constraining a species' range is characterized by these biologically informed parameters, hybrid models might predict dynamics better than correlative models based solely on environmental variables. One issue is whether correlated outputs from mechanistic models (as most are currently dependent on temperature) can predict distributions as well as less-correlated environmental variables.

CONCLUSION

Climate change, human land use, and species introductions have created a strong need for accurate models of species'

ranges. Already species are shifting ranges in response to changing climates in individualistic ways, meaning that we cannot just assume simple poleward shifts (Parmesan 2006). Novel climates are expected to form as multiple climate variables shift non-linearly across the globe (Williams & Jackson 2007). Our comparison has revealed that correlative and mechanistic models perform similarly at predicting current distributions, but predict differential responses to a uniform warming. Using hindcasting to test the range models will be essential to assessing whether correlative models are sufficient for predicting range dynamics. Furthermore, we need to improve the generality of mechanistic models while also extending the models to incorporate species interactions, dispersal limitations, geographic variation in genotypic and phenotypic traits, and adaptive evolution. Such efforts will require the collection of large amounts of data on physiologies, behaviors, and life histories throughout entire regions. At the same time, correlative models will be needed to suggest important mechanisms for consideration in developing mechanistic models and for unstudied organisms. Given the current rate of climate change, we should not need to wait too long to validate current model predictions under substantially altered conditions.

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SUPPORTING INFORMATION

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

Appendix S1 Supplementary methods.

Figure S1 A sensitivity analysis of the range predictions for *Sceloporus undulatus* to environmental data.

Figure S2 Range predictions for *Sceloporus undulatus* showing details of the model predictions.

Figure S3 Range predictions for *Atalopedes campestris* showing details of the model predictions.

Table S1 Model parameterizations.

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