Research

Ecography 37: 679–688, 2014
doi: 10.1111/j.1600-0587.2013.00600.x

Subject Editor: Miguel Araújo. Accepted 1 December 2013

Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change

Ana Ceia-Hasse, Barry Sinervo, Luís Vicente and Henrique M. Pereira

A. Ceia-Hasse (achferreira@fc.ul.pt), Centro de Biologia Ambiental and Centro de Estudos do Ambiente e do Mar, Faculdade de Ciências da Univ. de Lisboa, PT-1749-016 Lisboa, Portugal. – B. Sinervo, Dept of Ecology and Evolutionary Biology, Univ. of California, Santa Cruz, CA 95064, USA. – L. Vicente, Centro de Estudos do Ambiente e do Mar, Faculdade de Ciências da Univ. de Lisboa, PT-1749-016 Lisboa, Portugal. – H. M. Pereira, Centro de Biologia Ambiental, Faculdade de Ciências da Univ. de Lisboa, PT-1749-016 Lisboa, Portugal, and German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, DE-04103 Leipzig, Germany.

Uncertainty in projections of global change impacts on biodiversity over the 21st century is high. Improved predictive accuracy is needed, highlighting the importance of using different types of models when predicting species range shifts. However, this is still rarely done. Our approach integrates the outputs of a spatially-explicit physiologically inspired model of extinction and correlative species distribution models to assess climate-change induced range shifts of three European reptile species (*Lacerta lepida*, *Iberolacerta monticola*, and *Hemidactylus turcicus*) in the coming decades. We integrated the two types of models by mapping and quantifying agreement and disagreement between their projections. We analyzed the relationships between climate change and projected range shifts. Agreement between model projections varied greatly between species and depended on whether or not they consider dispersal ability. Under our approach, the reliability of predictions is greatest where the predictions of these different types of models converge, and in this way uncertainty is reduced; sites where this convergence occurs are characterized by both current high temperatures and significant future temperature increase, suggesting they may become hotspots of local extinctions. Moreover, this approach can be readily implemented with other types of models.

The projected impacts of global change on biodiversity show species extinctions, loss of natural habitat, and changes in the distribution and abundance of species and biomes over the 21st century (Pereira et al. 2010). Climate change is one of the most important drivers of biodiversity change (Bellard et al. 2012) and is affecting both the distribution and phenology of organisms (Parmesan 2006). Projections of change are essential for conservation planning (Thuiller 2007), but their accuracy needs to be improved to sustain ecosystem services and functions (Millennium Ecosystem Assessment 2005). However, the uncertainty level in projections of biodiversity change is greater than had been previously acknowledged (Pereira et al. 2012). This highlights the importance of using different types of models when predicting species range changes, which allows assessing uncertainty and allows identifying and correcting errors. However, this approach is still rarely undertaken (Leadley et al. 2010).

Global change impacts on biodiversity can be estimated through models that can be broadly classified into phenomenological or process-based models (Pereira et al. 2010). Most phenomenological models are correlative models relying on the establishment of statistical relationships between current species distributions and climate variables to project the future distribution of a species under projected environmental change (Heikkinen et al. 2006). Process-based models determine the mechanistic interactions between the growth or fitness of an organism, and its environment, using theoretical inferences, experiments, or both (Araújo 2009).

Understanding both the strengths and limitations of correlative models, and their conceptual basis, is essential for their correct application (Araújo and Peterson 2012). The relative simplicity of correlative models is one of their main advantages, since they can be used for any species for which there are reliable distribution data and the corresponding environmental variables (Morin and Thuiller 2009). Correlative models can implicitly capture many complex ecological responses (Elith et al. 2010), but may fail to predict range dynamics accurately (Buckley et al. 2010). This is because they are based on correlations between current climates and species distributions, and if climate change leads to new combinations of the states of those environmental variables many future climates will probably lack current analogs (Williams and Jackson 2007). Correlative models have been used extensively for a large number of groups of organisms and in a wide variety of contexts, spanning conservation, ecological and evolutionary questions (Zimmermann et al. 2010, Araújo and Peterson 2012). These include the assessment of the impacts of climate change on the distribution of reptiles in the future (Araújo et al. 2006, Carvalho et al. 2010).

Process-based models require much more natural history and physiological knowledge when compared to correlative models (Thuiller 2007); their parameterization is limited by data availability and their success in predicting range limits depends on identifying the key processes that limit distributions (Elith et al. 2010). On the other hand, they highlight those processes involved in determining range boundaries (Morin and Thuiller 2009) and are expected to be more robust under new environmental conditions, and in new places (Elith et al. 2010).

Defining an unambiguous distinction between correlative and process-based models may however not be straightforward, since most models will be intermediate in what regards the explicit inclusion of processes (Dormann et al. 2012). One such model that defines the interaction between organisms and their environment based on theoretical inferences (Araújo 2009) is the model developed by Sinervo et al. (2010) that predicted extinction rates for reptiles due to climate warming using a simple physiologically inspired model of extinction. Being ectothermic, reptiles are an excellent model system for explicitly incorporating such constraints when modeling range shifts in response to climate change, because their physiology and distribution are more directly influenced by environmental temperature than in endothermic vertebrates (Buckley et al. 2012).

The model proposed by Sinervo et al. (2010) assumes that restriction in activity due to hot weather during lizards' breeding period may lead to population extinction by constraining foraging and therefore the accumulation of the amount of energy that is necessary for reproduction. Under this rationale, they developed the model based on the observation that lizard population extinctions in Mexico were related with an increase in maximum air temperature during the breeding period (Tmax) and with the physiologically active body temperature of the animals (Tb). The duration of restriction in activity (Hr) was also related with the increase in Tmax. They established a relationship to calculate Hr using Tmax and Tb, and determined the maximum value of Hr that populations can sustain without going extinct, for 34 lizard families worldwide (see Methods in this paper and Sinervo et al. 2010). In this model, Sinervo et al. (2010) explicitly postulate a process that leads to extinction, which is restriction in activity time caused by high environmental temperatures. The model does not go all the way to compute energy budgets or fecundity constrained by restriction in activity, but the processes included in the model are explicitly stated, and explicitly modeled. They established a link between Tb, Tmax, and restriction in activity, which was assessed by operative model temperatures. The link between restriction in activity time and reduced fecundity leading to increased extinction risk, is implicit.

This differs from more detailed physiological mechanistic models, that solve coupled energy and mass balance equations to establish an explicit link between the energy and water requirements of an organism, and environmental availability (Mitchell et al. 2008, Kearney and Porter 2009, Kearney et al. 2010). In these models, it is possible to infer range constraints and model potential distributions by reconstructing microclimate conditions (Kearney and Porter 2009). This approach includes microclimate and animal models that incorporate morphology, physiology and behavior to reconstruct microclimates across landscapes, and is implemented in the Niche Mapper system (Porter and Mitchell 2006). It has become a standard of mechanistic models that deal with heat and mass transfer, namely for reptiles (Huang et al. 2013, Mitchell et al. 2013), having also recently been used to provide the environmental input for a dynamic energy budget model (Kearney 2012).

Given the relative advantages and disadvantages of different types of models, none can be considered better than the other per se (Dormann et al. 2012). Moreover, several authors have pointed out that the use of different types of models provides independent lines of evidence that may confer accuracy to projections where they converge (Hijmans and Graham 2006, Kearney and Porter 2009, Morin and Thuiller 2009). This procedure has been used to predict range shifts for both plants (Hijmans and Graham 2006, Morin and Thuiller 2009) and several animal groups (e.g. lizards: Buckley et al. 2010, mammals: Kearney et al. 2010, butterflies: Buckley et al. 2010, 2011), as well as for invasive species (Elith et al. 2010). The most common approach is to apply the models independently to the same raw data and then comparing models' performance in predicting current distributions, and by comparing range shifts projected into the future either qualitatively or quantitatively (Morin and Thuiller 2009, Buckley et al. 2010, Kearney et al. 2010). Other approaches include incorporating species-specific physiological information into correlative models (Buckley et al. 2011), using the outputs of a mechanistic model as input in correlative models (Hijmans and Graham 2006, Elith et al. 2010), or applying ecophysiological bioclimatic modeling techniques (such as the one implemented in CLIMEX; Kitricos and Leriche 2010). A recent approach consists in using the outputs of correlative models as input in mechanistic models. These coupled ecological niche-population models link habitat suitability (the correlative ecological niche model output) to demographic models of population dynamics that incorporate survival, growth, reproduction and dispersal processes. In this way they account for important biological and landscape processes, and their interactions, potentially providing improved estimates of extinction risk and range shifts under climate change (Fordham et al. 2013).

In this paper we present an approach that combines two types of models with the aim of reducing uncertainty in projections of change. Furthermore, we show how this approach can contribute to a better understanding of the constraints underlying species range limits, and inform the further development of both types of models and hybrid models. Our modeling approach consists of using a simple physiologically inspired model of extinction for comparing with the projections of a correlative model, and of assessing species range shifts by comparing projected future distributions with the distribution that is observed, instead of using the distribution predicted for a baseline period. We test this approach with range shifts of European reptile species projected for the coming decades due to climate change. We chose three species: *Lacerta lepida* (ocellated lizard), *Iberolacerta monticola* (Iberian rock lizard), and *Hemidactylus turcicus* (Mediterranean house gecko). The species were chosen because they show different trends in projections of distribution shifts (Araújo et al. 2006, Sinervo et al. 2010). *Iberolacerta monticola* is predicted to contract, *H. turcicus* is predicted to expand, and *L. lepida* is predicted to either contract or expand depending on the combination of correlative modeling technique, climate general circulation model and emissions scenario chosen (Araújo et al. 2006).

Material and methods

Species data

For the correlative modeling, we used species observed distribution data in Europe at the spatial resolution of 50 × 50 km, obtained from Gasc et al. (1997). For the physiological model, we used average body temperature (Tb) data, obtained for each species from the available literature: *Lacerta lepida*: 27.8°C (Mateo 2009); *Iberolacerta monticola*: 29.4°C (Martín 2009); *Hemidactylus turcicus*: 31.4°C (Huey et al. 1989).

Climate data

Climate variables were derived from gridded average monthly values of temperature (°C) and precipitation (mm) in Europe (Mitchell et al. 2004) and include: mean annual temperature, mean temperature of the coldest month, mean temperature of the warmest month, mean annual precipitation, and mean precipitation from July to September for the correlative model (Araújo et al. 2006), and mean maximum temperature in the reproduction months of each species for the physiological model (Sinervo et al. 2010). These variables were averaged for 1961–1990 (baseline period) and for 2020–2050 (future period). Climate projections for 2020–2050 were derived from the HadCM3 general circulation model (GCM) with the IPCC-SRES A2 scenario (Nakicenovic and Swart 2000, Mitchell et al. 2004). We chose these GCM and scenario to keep coherence with Araújo et al. (2006) and Sinervo et al. (2010) since these were the studies upon which we based our choice of species. The HadCM3 GCM and the A2 scenario were the only common to both studies.

Correlative modeling

Species distributions were modeled using the techniques implemented in BIOMOD (artificial neural networks, classification tree analysis, generalized additive models, generalized boosting model, generalized linear models, mixture discriminant analysis, multiple adaptive regression splines, and Breiman and Cutler's Random Forest for classification and regression) (Thuiller 2003, Thuiller et al. 2009) run within R (ver. 2.11.1; R Development Core Team). We calibrated the models with a 70% random sample of the observed data and predictive accuracy was evaluated on the remaining 30% of the data using the area under the curve of the receiver operating characteristic curve, Cohen's Kappa statistic, and the true skill statistic (Fielding and Bell 1997). The modeled distributions chosen for integration with the physiological model were the ones with the highest predictive accuracy for the baseline period (1961–1990). We considered two extreme options for dispersal: no dispersal and full dispersal. In the no dispersal option, the species are unable to disperse and establish in new areas, and in the full dispersal option, the species have no constraints to dispersal. We chose these options instead of an intermediate dispersal capacity because we wanted to calculate the full span of future potential ranges.

Physiological modeling

We used the spatially-explicit physiologically inspired model of extinction proposed by Sinervo et al. (2010). Since this model is still relatively novel, we provide an expanded explanation on how it was developed (see also Fig. 1). The rationale behind this model is that when environmental temperatures are too high, lizards retreat to cool refuges. However, in this way activity time will be restricted, which will limit foraging, thereby constraining costly metabolic functions such as growth, maintenance, and reproduction, and thus ultimately undermine population growth rates and raise extinction risk. The critical period during which restriction in activity is considered to govern extinction risk is the reproduction period.

Under this approach, the status of a population at a given georeferenced site is modeled as persistent or non-persistent by firstly calculating the hours of restriction in activity (Hr). Hr is computed using the mean daily maximum air temperature during the months of reproduction (Tmax) at that site, and the physiologically active body temperature of the lizards (Tb) (see below). Hr is then compared to a threshold value, which is the maximum number of hours of restriction in activity (Hr_limit). If Hr_limit is exceeded, the population at that site is considered to go extinct.

Step 1: observing an empirical relationship between extinction, Tmax and Tb

Sinervo et al. (2010) compared surveys for 48 *Sceloporus* lizard species at 200 sites in Mexico and observed that 12% of populations had gone extinct between 1975 and 2009. In these comparisons, they excluded the cases in which habitat modification caused extinctions, including only sites characterized by intact habitat as in the historical surveys. The observation that the local extinctions were correlated with the rate of change in Tmax during the breeding season, and with low Tb, originated the development of the model. It suggested that extinctions could have been driven by reduced activity under hot weather leading to insufficient energy accumulation and consequent impaired reproduction.

Step 2: finding a functional relationship between Hr, Tmax and Tb

To assess if extinction could be related to restriction in activity due to hot weather, Sinervo et al. (2010) compared two locations in Mexico from where the lizard species *Sceloporus serrifer* had recently gone extinct, with two other locations where this species was persistent. They deployed thermal models that mimic the thermal properties of a basking lizard to record operative model temperatures (Te) at the two

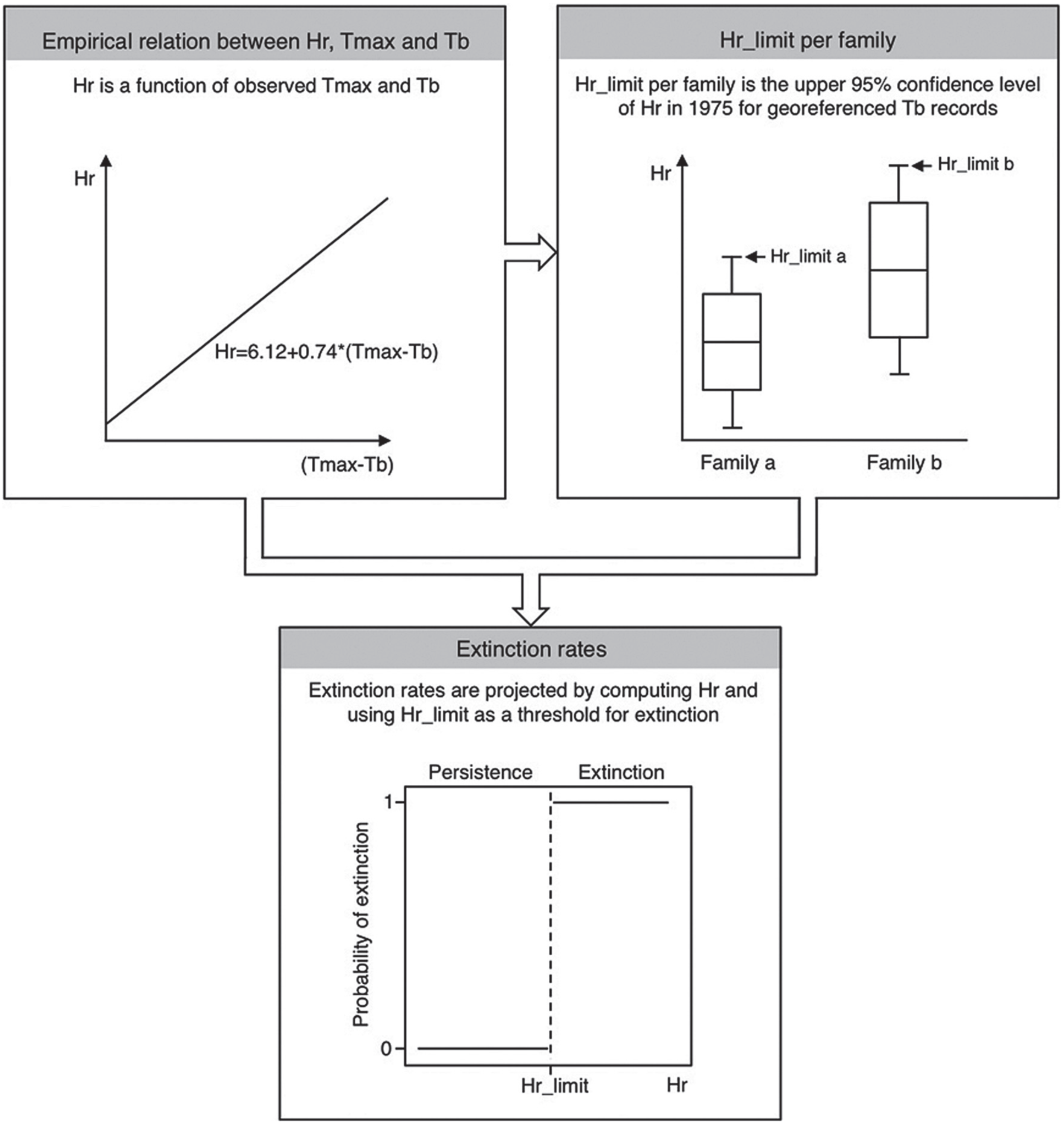

Figure 1. Schematic representation of the model proposed by Sinervo et al. (2010). See text for details; for a full description of the model see the original paper and corresponding supplementary materials. Hr: hours of restriction in activity; Tmax: maximum air temperature during the months of reproduction; Tb: physiologically active body temperature; Hr_limit: threshold for extinction (Hr above which populations are assumed to go extinct). For thermoconformers that maintain Tb close to air temperature (Tair), the model is modified by computing Hr as the cumulative number of hours that Tair is above Tb, assuming a sine wave for Tair between Tmin and Tmax (24-h period) (Sinervo et al. 2010). Otherwise the method is the same.

extinct and the two persistent sites. They recorded average Te every hour over a 4-month period from January 2009, and determined the cumulative number of hours each day that Te was above the Tb of *S. serrifer*. Assuming that during this period animals would be inactive, this corresponds to the hours of restriction in activity (Hr). They also observed that Hr was positively correlated with Tmax, which had significantly increased over the last 36 yr in the same months. Sinervo et al. (2010) determined the relationship between Hr assessed by Te, and Tmax. They related Hr to observed Tmax on a daily basis, and fitted a significant linear regression equation. Then they standardized this equation in terms of Tb, to obtain Hr as a function of Tmax and Tb, given by: Hr = 6.12 + 0.74 × (Tmax – Tb) (Eq. S2 in Sinervo et al. 2010). This formula can be extended to any species of lizard, given data on Tb.

Step 3: calibrating Hr_limit: extending the model to other Sceloporus species

Hr measured at persistent versus extinct sites of *S. serrifer* suggested that the maximum Hr for *S. serrifer*, above which extinction would occur, were 4 h (Sinervo et al. 2010). To extend the model to other *Sceloporus* species, Sinervo et al. (2010) calibrated that value using the local extinction data from the resurveyed sites in Mexico. They computed Hr at each of those sites using the equation presented above, the Tb of each species, and Tmax in 2009. To determine the extinction threshold (Hr_limit), they varied Hr_limit from 1 to 12 h in 0.1 h increments, and computed the overall fit of the model, by calculating the deviations of model predictions from the observed data. Based on this procedure, a value of Hr_limit of 3.85 h provided the best fit between observed and predicted extinctions.

Step 4: generalizing the model to other lizard families

Sinervo et al. (2010) then obtained extinction projections for 34 lizard families with geo-referenced Tb records from 1216 lizard populations. To do so, they estimated an Hr_limit for each family, using a best-fit procedure similar to the one used for the Mexican *Sceloporus* lizards (and thereby scaling Eq. S2 to each family). They computed the Hr each population would sustain in 1975, given Tb and Tmax during the breeding period in 1975 at each of the georeferenced sites, and for each family they used the upper 95% confidence level of Hr as the extinction threshold.

Step 5: validating the model globally

Sinervo et al. (2010) tested the global generality of their model by verifying the concordance between the distributions of current observed local extinctions, and local extinctions predicted by the model, in lizard populations from families in four other continents, besides family Phrynosomatidae in North America. To do this they used data of observed local extinctions from published records, and resurveys of known lizard populations, and compared them with the model predictions, obtained using the family-specific Hr_limit calibrations. In this analysis, disturbed sites were excluded and they focused on sites with intact habitat.

Step 6: projecting extinctions in the future

Besides calculating extinctions for 2009, Sinervo et al. (2010) used the physiological model of extinction as described above to compute extinction probabilities for 2050 and 2080.

Step 7: implementing the physiological model of extinction under our approach

In the present work, we modeled each species' persistence or non-persistence in 2020–2050 at each grid-cell where it is currently present. We used Tmax at each grid-cell and the corresponding species' Tb to compute Hr in each of those grid-cells, using the method developed by Sinervo et al. (2010). We computed species-specific extinction thresholds using the known distribution of each species and estimating Hr_limit as the upper 95% confidence level of Hr, following the method used by Sinervo et al. (2010). We have also used the physiological model to project species viability or non-viability at the grid-cells where the correlative model had projected colonizations. Being a model of extinction that incorporates only the upper limits of thermal constraints, the model developed by Sinervo et al. (2010) is not appropriate to model species distributions per se. Instead, we have used it to compare ecophysiological limits to persistence with projections of the correlative model. In this way, our modeling approach hybridizes outputs from the two different models.

Assessing species distribution shifts

We assessed species range shifts by comparing projected future distributions with observed distributions. This can be considered as a filtered approach, in opposition to a non-filtered one, in which to assess range shifts, future distributions are compared with the distribution predicted for the baseline period. Accordingly, for any grid-cell, in the non-filtered approach an extinction is considered as such when the model predicts absence in the future and presence in the predicted current distribution, regardless of whether the species is present or absent in the observed distribution. In contrast, in the filtered approach, extinctions are only considered as such if the species is present in the observed distribution. The same rationale applies to colonizations: in the filtered approach, colonizations at any given site are only considered as such, if the species is absent from that site in the observed distribution. We developed a classification scheme for the events projected in the future following these approaches (Table 1). The filtered approach is important for model integration because it establishes a common baseline – the observed distribution – against which to classify events projected in the future. This approach also has the advantage of avoiding estimating extinctions from areas where the species might not occur, and of estimating colonizations in areas where the species is already present.

Table 1. Classification scheme of events projected in the future according to the filtered and non-filtered approaches. Species presence is denoted by '1', and species absence is denoted by '0'. Events with a † indicate that even though the presence/absence status is predicted to change from the observed to the future distribution, the prediction for the current period is inconsistent with the observed status. In those cases, we chose to make the cautious option of classifying the future event with the same status as in the observed distribution.

Observed distribution	Predicted distribution		Classification of future event	
	Current	Future	Non-filtered	Filtered
1	1	1	Persistence	Persistence
		0	Extinction	Extinction
	0	1	Colonization	Persistence
		0	Absence	Persistence †
0	1	1	Persistence	Absence †
		0	Extinction	Absence
	0	1	Colonization	Colonization
		0	Absence	Absence

Integrating models

We considered that the physiological model supported the projections of the correlative model where the projections were the same for both models. In this way, for any grid-cell, the physiological model supports extinctions projected by the correlative model when both models project extinction in that grid-cell. Colonizations are scored as supported when the physiological model projects the species viability in a grid-cell where the correlative model has projected a colonization. Species range shifts were quantified for each species by calculating the percentage of extinctions and colonizations projected relative to the total number of grid-cells with observed presences. Agreement between models was calculated as the percentage of extinctions and colonizations supported by the physiological model relative to the total number of extinctions and colonizations (respectively) projected by the correlative model.

Associations between climate and species range shifts

To analyze the relationships between climate and the events projected by each model in the future, and how climate influences agreement and disagreement between the models, we used generalized linear models (GLMs). Current climate and climate variation between future and current periods (Araújo et al. 2006) were used as predictors, because we wanted to disentangle the effect of these two sets of variables. From the correlative model, we selected the relevant variables using the importance of each variable, given by BIOMOD (Thuiller 2003, Thuiller et al. 2009). For each species, we averaged variable importance across all variables, and the variables with an importance above the mean value were selected (Capinha and Anastácio 2011).

We analyzed how climate differs between sites where different events were projected, using the following comparisons for each species (Table 3): extinctions versus persistences projected by the physiological model; extinctions versus persistences projected by the correlative model; extinctions versus persistences projected by both models; colonizations versus absences projected by the correlative model; colonizations projected by the correlative model and not supported by the physiological model versus colonizations supported by the physiological model.

Each comparison was modeled as a binary response variable, and thus GLMs were fitted by specifying a binomial distribution and a logistic link function (Crawley 2007). The probability of an event was modeled as a linear function of the climate variables. We used backwards elimination of non-significant factors to check whether removing one or more explanatory variables would improve the GLM, by examining the differences in the Akaike's information criterion (AIC) values resulting from removing different explanatory variables. Only those variables whose regression coefficient estimates were significant at the 0.05 confidence level (z-test) and whose removal would cause a decrease in Akaike weight (Burnham and Anderson 2002), and thus a worse fit, were maintained. We computed standardized regression coefficients to show the relative importance of significant variables (Gelman and Hill 2006). We fitted all models with the glm and step functions from the stats package within R (ver. 2.11.1; R Development Core Team).

Although the temperature above which extinctions are predicted by the physiological model can be determined simply by reversing the equation for Hr at the threshold temperature, the procedure detailed above enabled us to identify the relative importance of current versus future temperature on the probability of an event being projected by the physiological model, besides assessing the influence of these two predictors on agreement and disagreement between the models.

Results

Species range shifts and support by the physiological model

The extinction thresholds (Hr_limit) for each of the species were the following: 3.5 h for *Lacerta lepida*, 2.3 h for *Iberolacerta monticola*, and 10.5 h for *Hemidactylus turcicus*.

Under the no dispersal assumption, *Lacerta lepida* is projected to lose from 8% of its current distribution up to a maximum of 39% (extinctions projected by the correlative model and supported by the physiological model and total extinctions projected by the correlative model, respectively) (Table 2). The physiological model also projects 19% extinctions in areas where the correlative model does not project extinctions. The extinctions projected by both models are in the west and southernmost part of the species' current distribution while the correlative model alone also projects extinctions in the south and mostly in the north and northeast parts of the species' current range (Fig. 2). When full dispersal is considered, *L. lepida* is projected to colonize between 29 to 33% new areas relative to its current distribution, and mainly to the north of its current range (colonizations projected by the correlative model and supported by the physiological model and total colonizations projected by the correlative model, respectively). The colonizations projected by the correlative model and not supported by the physiological model are located in the Iberian Peninsula and in the Balkan Peninsula.

Iberolacerta monticola is projected to lose all its range according to the correlative model if dispersal is not considered (Table 2). However, the physiological model does not support these extinctions. When dispersal ability is considered, the correlative model does not project any colonizations (Fig. 3).

Hemidactylus turcicus is projected to expand its distribution. The correlative model projects 7% extinctions but none are supported by the physiological model, which projects no extinctions (Table 2). Regarding colonizations, *H. turcicus* is projected to almost double its current range. This species is projected to colonize new areas into the north along its longitudinal range that correspond to 92% of its current range, and these projections are fully supported by the physiological model (Fig. 4).

Agreement between models

Agreement between model projections varies greatly between species and is dependent on whether dispersal ability is considered or not (Table 2). The correlative model projects

Table 2. Percentage of extinctions and colonizations projected for each species for 2020–2050.

		Lacerta lepida	*Iberolacerta monticola*	*Hemidactylus turcicus*
Extinctions	Projected by correlative	39	100	7
	Projected by physiological	27	0	0
	Projected by correlative and supported by physiological	8	0	0
Colonizations	Projected by correlative	33	–	92
	Projected by correlative and supported by physiological	29	–	100

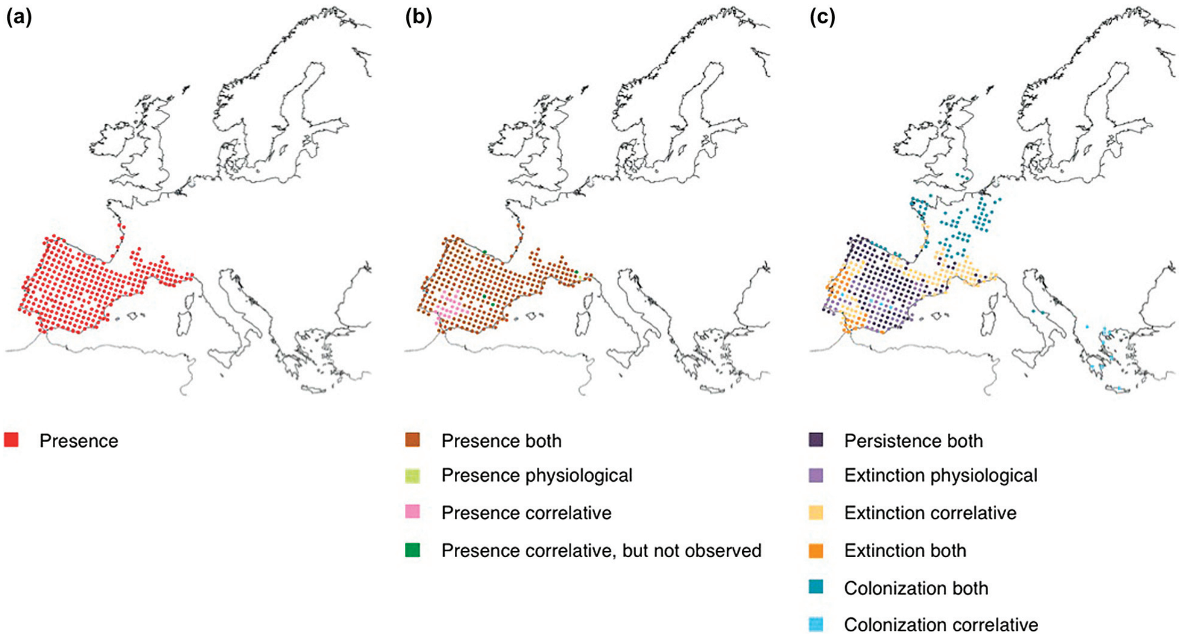

Figure 2. Distribution maps for *Lacerta lepida*. (a) Observed distribution, (b) distribution predicted for the baseline period, and (c) distribution projected for the future, for both models superimposed upon each other and upon the observed distribution to illustrate agreement and disagreement between the models.

a higher level of extinctions than the physiological model for all species. Agreement between the extinctions projected by the correlative model and the physiological model is low (20% for *Lacerta lepida* and 0% for *Iberolacerta monticola* and *Hemidactylus turcicus*). The correlative model also projects a high level of colonizations for *L. lepida* and *H. turcicus*, which are well supported by the physiological model (87% support for *Lacerta lepida* and 100% for *Hemidactylus turcicus*).

Associations between climate and species range shifts

Using the criterion of mean value of variable importance given by BIOMOD, the predictor variables selected from the correlative model were: temperature of the coldest month (T_C) and precipitation between July and September (P_{JS}) for *Lacerta lepida*; and annual temperature (T_A) and annual precipitation (P_A) for *Hemidactylus turcicus*. From the physiological model the climate variable was temperature in the reproduction months (T_R). We excluded *Iberolacerta monticola* from this analysis because the correlative model projected a total loss of the species current range, while projecting no colonizations, and the physiological model did not project any extinctions.

For *Lacerta lepida*, both T_R and ΔT_R are higher at the sites where the physiological model projected extinctions (Table 3). The sites where the correlative model projected extinctions have higher T_C and lower P_{JS}, and will become hotter and drier in the future (higher ΔT_C and higher ΔP_{JS}).

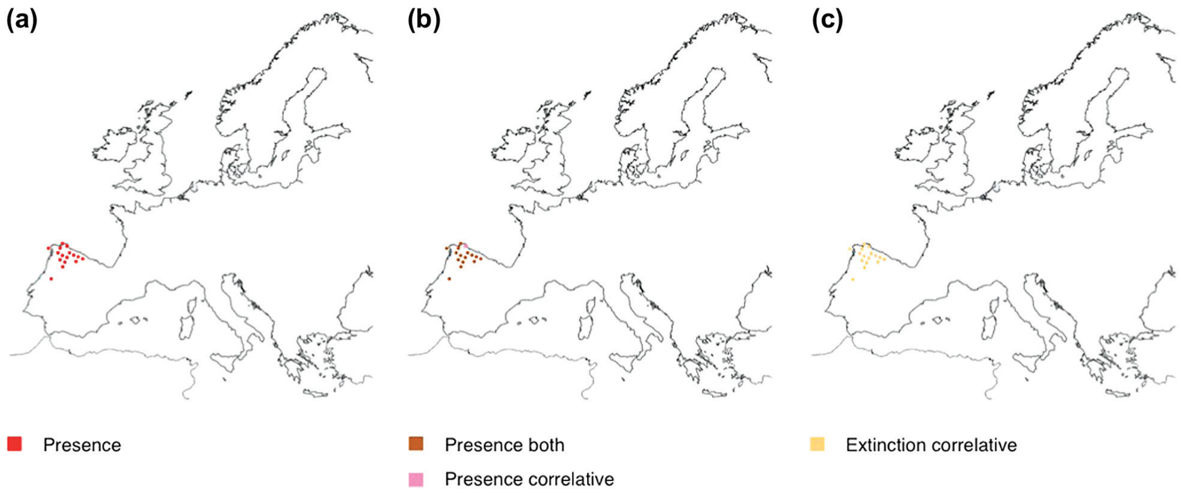

Figure 3. Distribution maps for *Iberolacerta monticola*. (a) Observed distribution, (b) distribution predicted for the baseline period, and (c) distribution projected for the future, for both models superimposed upon each other and upon the observed distribution to illustrate agreement and disagreement between the models.

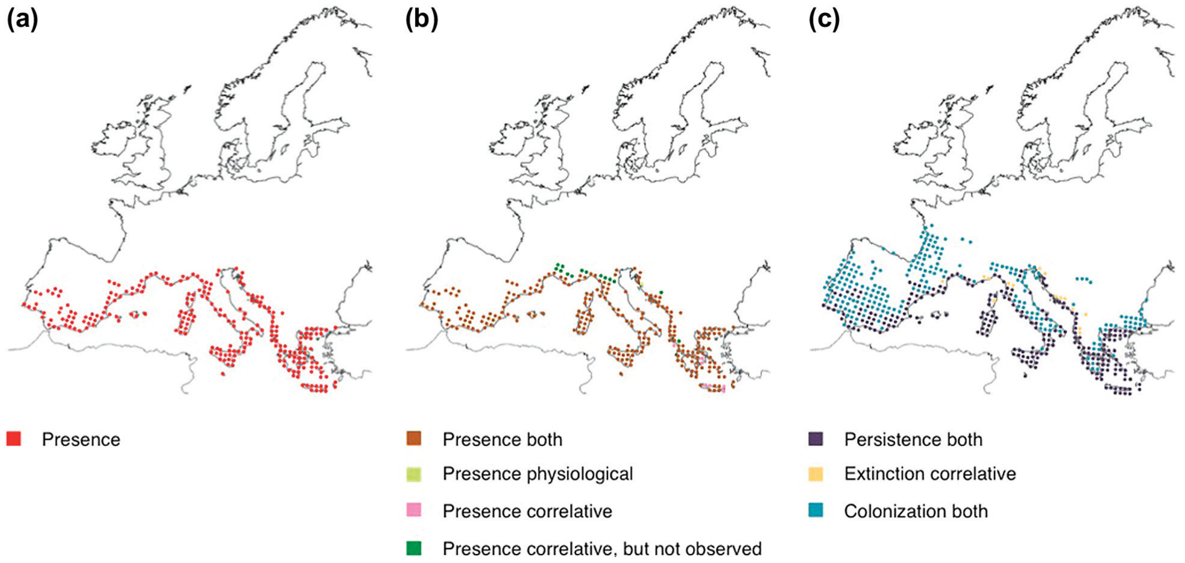

Figure 4. Distribution maps for *Hemidactylus turcicus*. (a) Observed distribution, (b) distribution predicted for the baseline period, and (c) distribution projected for the future, for both models superimposed upon each other and upon the observed distribution to illustrate agreement and disagreement between the models.

Sites where both models projected extinctions are characterized by having higher T_C, higher ΔP_{JS}, higher T_R, and higher ΔT_R than the sites where both models projected persistence. The correlative model projected colonizations where T_C is higher but will not increase significantly in the future, and where P_{JS} is higher but will decrease more in the future. Both T_R and ΔT_R are higher where the physiological model did not support the colonizations projected by the correlative model.

For *Hemidactylus turcicus*, the physiological model did not project any extinctions, and supported all the colonizations projected by the correlative model. T_A, ΔT_A and P_A are lower where extinctions were projected than where persistence was projected by the correlative model (Table 3). Sites where colonizations were projected differ from sites where absences were projected in that T_A, ΔT_A and ΔP_A are higher where colonizations were projected.

Discussion

The physiological model suggests that in the west and southernmost part of *Lacerta lepida*'s current distribution, where extinctions projected by the correlative model are supported, future temperatures during the reproduction period may be too high to allow population persistence. Sites where this convergence occurs are characterized by both current high temperatures, and significant future temperature increase. The same rationale applies to the sites where colonizations projected by the correlative model are not supported by the physiological model. At these sites, even if other climatic factors would allow the presence of *Lacerta lepida*, high temperatures during the reproduction period would prevent the colonization of these new areas.

For *Iberolacerta monticola* and *Hemidactylus turcicus*, the physiological model does not support any of the extinctions

Table 3. Climate variables and significant regression coefficients ($p < 0.05$) for each comparison of events projected, from generalized linear modeling.

	Explanatory variables					
	Temperature coldest month		Precipitation July–September		Temperature reproduction months	
Species and events compared	Current	Change	Current	Change	Current	Change
Lacerta lepida						
Extinction vs persistence physiological					2.44	1.97
Extinction vs persistence correlative	1.04	0.36	−0.91	0.45		
Extinction vs persistence both models	8.43	n.s.	n.s.	2.99	4.21	3.87
Colonization vs absence correlative	1.85	n.s.	0.72	1.51		
Colonization not supported vs supported					9.43	5.45
	Annual temperature		Annual precipitation			
	Current	Change	Current	Change		
Hemidactylus turcicus						
Extinction vs persistence correlative	−8.96	−6.07	−2.36	n.s.		
Colonization vs absence correlative	7.62	2.49	n.s.	0.39		

projected by the correlative model, and for *H. turcicus* it supports all the colonizations projected by the correlative model. This suggests that even though temperature is projected to increase at these places, high temperatures during the reproduction period in the future would not hinder population persistence in currently occupied (*I. monticola* and *H. turcicus*) or in newly occupied areas (*H. turcicus*). The analysis of the associations between climate and range shifts projected by the correlative model also indicates that high temperature is not the most limiting factor, neither for colonizations nor for extinctions.

Accounting for geographic variation in reproduction dates and body temperatures could refine the predictions of the physiological model (Sinervo et al. 2010, 2011, Clusella-Trullas and Chown 2011) and help explain some of the inconsistencies found in the present study. Habitat characteristics and behavioural thermoregulation in ectotherms can also moderate the effects of climate warming (Kearney et al. 2009) and thus could also be considered (Sinervo et al. 2010, 2011, Clusella-Trullas and Chown 2011), as well as including other climatic data and linking them to demography (Sinervo et al. 2011).

The use of several climate general circulation models (GCM), emissions scenarios, as well as bioclimatic statistical models, is a way of assessing uncertainty in projections of change and has been recommended by several authors (see Beaumont et al. 2007 and references therein). In this study, we chose to use one GCM and one emissions scenario, because our intention was to evaluate and exemplify the use of different models under a common modeling framework. Input from more GCMs and/or scenarios could nevertheless be easily incorporated. Our modeling approach could be further enriched by refining the spatial resolution of the analysis for those areas identified as vulnerable (Carvalho et al. 2010) but also where stronger inconsistencies between the models were found. Other factors shaping species responses to environmental change should be considered, such as biotic interactions (Jankowski et al. 2013), and the synergistic effects between climate change and land use change (Pereira et al. 2010).

Most importantly, the physiological model was developed under the assumption that restriction in activity time due to hot weather in the breeding period would increase extinction risk through energetic deficits that reduce reproductive output. This assumption is supported by independent studies (Huey et al. 2010) showing that lizard annual activity times are positively correlated with annual fecundity (Adolph and Porter 1993). However, in contrast with correlative models, for which there are independent model-data comparisons (Araújo et al. 2005), the hypothesis proposed by Sinervo et al. (2010) has not been proven empirically, and therefore still needs validation with independent datasets.

The extinction model developed by Sinervo et al. (2010) incorporates only thermal constraints, but there are several causes for extinction, which are not necessarily mutually exclusive (Koch and Barnosky 2006). A physiological model can be most useful in indicating where a species may not be able to exist (Elith et al. 2010). By focusing exclusively on the upper bounds of thermal constraints, the extinction model used here can only provide information on the impact of high temperatures on persistence, under future temperature increase as indicated by climate change projections (IPCC 2007). In this context, using the physiological model to assess the colonizations projected by the correlative model allows highlighting potential places where temperatures in the future may be so high they would impair per se the persistence of populations, were individuals able to reach those areas. This could be an asset for conservation planning, such as the design of reserves or habitat restoration efforts. We also assessed species range shifts by comparing the projected future distributions with the observed distribution. This approach avoids estimating extinctions from areas where the species might not occur and colonizations in areas where the species is already present. Therefore, it is more realistic and hence also more useful for conservation planning (Araújo et al. 2011).

Using different types of models in conjunction can inform the selection of variables and processes to be included (Buckley et al. 2010) and is essential to understand the limits to species distributions (Austin et al. 2009). Considering the discussed advantages and disadvantages of the different models and the urgency of producing accurate predictions of biodiversity response to global environmental change, we suggest that the best strategy currently available is the use of different types of models under a common modeling framework. Other authors have highlighted the importance of such an approach (Buckley et al. 2010, Kearney et al. 2010, Dormann et al. 2012), but much work still needs to be done. The main objective of the present work was to suggest an approach to accomplish that, and which can easily be implemented with other models. Since different models rely on different assumptions, their predictions can be considered to be complimentary (Morin and Thuiller 2009). In this way the reliability of predictions is greatest and uncertainty in projections is reduced where the models' predictions converge.

Acknowledgements – This work was supported by grant PTDC/AACAMB/114522/2009 from Fundação para a Ciência e a Tecnologia. BS was supported by IOS-1022031 from the U.S. National Science Foundation. We thank Luís Borda de Água and Thomas Merckx for comments.

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