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The ability of climate envelope models to predict the effect of climate change on species distributions

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Abstract

Climate envelope models (CEMs) have been used to predict the distribution of species under current, past, and future climatic conditions by inferring a species' environmental requirements from localities where it is currently known to occur. CEMs can be evaluated for their ability to predict current species distributions but it is unclear whether models that are successful in predicting current distributions are equally successful in predicting distributions under different climates (i.e. different regions or time periods). We evaluated the ability of CEMs to predict species distributions under different climates by comparing their predictions with those obtained with a mechanistic model (MM). In an MM the distribution of a species is modeled based on knowledge of a species' physiology. The potential distributions of 100 plant species were modeled with an MM for current conditions, a past climate reconstruction (21 000 years before present) and a future climate projection (double preindustrial CO_2 conditions). Point localities extracted from the currently suitable area according to the MM were used to predict current, future, and past distributions with four CEMs covering a broad range of statistical approaches: Bioclim (percentile distributions), Domain (distance metric), GAM (general additive modeling), and Maxent (maximum entropy). Domain performed very poorly, strongly underestimating range sizes for past or future conditions. Maxent and GAM performed as well under current climates as under past and future climates. Bioclim slightly underestimated range sizes but the predicted ranges overlapped more with the ranges predicted with the MM than those predicted with GAM did. Ranges predicted with Maxent overlapped most with those produced with the MMs, but compared with the ranges predicted with GAM they were more variable and sometimes much too large. Our results suggest that some CEMs can indeed be used to predict species distributions under climate change, but individual modeling approaches should be validated for this purpose, and model choice could be made dependent on the purpose of a particular study.

Keywords: bioclim, climate change, domain, envelope models, GAM, maxent, species distributions

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Introduction

A number of species have been affected by recent climatic change, with changes in phenology and ranges expanding towards higher latitudes and altitudes (e.g. Parmesan & Yohe, 2003; Root *et al*., 2003). Understanding how species will respond to projected future climate change is of fundamental importance for effective management and conservation of biodiversity (Hannah *et al*., 2002). Likewise, insight into the distributions of species during past climates can help to understand current patterns of species distributions and genetic variation (Hugall *et al*., 2002; Peterson *et al*., 2004; Graham *et al*., 2006; Ruegg *et al*., 2006). Predicting species ranges for different climates is commonly done with 'climate envelope models' (CEMs) that use the current geographic distribution of a species to infer its environmental requirements. Based on these requirements, a species' geographic distribution for the current, or for past or future climates is predicted. A recent

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compilation of such studies on the effect of projected climate change indicates that an alarming number of species may lose a large part of their range and become 'committed to extinction' (Thomas *et al.*, 2004).

There are some obvious cases of species that with climate change should lose parts of their range, such as mountain-top endemics, for which warming would seem highly threatening (Theurillat & Guisan, 2001; Williams *et al.*, 2003). However, a general tendency of species ranges to get smaller with climate warming is counter-intuitive because there are more species in warm areas than in cold areas. The predicted trend towards reduction in range sizes that Thomas *et al.* (2004) found may have been caused by a biased selection of the species or regions studied. Another possibility is that some CEMs are biased and tend to underestimate range sizes under future climates. Thuiller *et al.* (2004) pointed out the problem of strong variation between CEM predictions of future distributions.

A persistent problem with CEMs is the difficulty in evaluating predicted distributions under different climates (i.e. reconstructions of past climates or projections of future climates). Whereas predictions under current circumstances can be tested using independent model training and testing datasets (Fielding & Bell, 1997), such a direct assessment cannot be done for future climates, for which there are no observed data. Using the fossil record, such tests are in principle possible for past climates (Martínez-Meyer *et al.*, 2004), but the number of sites from which fossils of a species are known for a given time period is often very small, and the available climate reconstructions are coarse and uncertain. Araújo *et al.* (2005a, b) used recent changes in the distribution of breeding birds in Britain and found reasonable agreement between observed and predicted changes over a period of 20 years. Such studies are useful but may be hampered by the confounding effect of changes in species' ranges for reasons unrelated to climate change (e.g. anthropogenic land cover change). Finally, some support for the use of CEMs for climate change studies can be drawn from successes in predicting a species range from data from one continent to another, as has been done for introduced invasive species (Peterson, 2003; Thuiller *et al.*, 2005).

There are a number of reasons why a prediction of a species' distribution after climate change could be less accurate than such a prediction for current climatic circumstances (Davis *et al.*, 1998; Guisan & Thuiller, 2005). CEMs are 'statistical' models that do not attempt to describe 'cause and effect' between model parameters and response (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003; Kearney & Porter, 2004). For example, the inferred environmental requirements are dependent on the climatic conditions that are currently available on the landscape. A species may be well adapted to a combination of rainfall and temperature that currently does not exist in the region where it occurs. If new combinations of climatic variables appear in the future, or if entirely new conditions occur (e.g. higher rainfall than currently observed anywhere), a statistical model may incorrectly classify such environments as unsuitable. The degree to which different statistical models may be affected by these problems has proved difficult to determine, but large variability among different CEM approaches used to predict species distributions under a projected future climate have been reported (Thuiller, 2003, 2004; Pearson *et al.*, 2006).

Here, we present a new framework for evaluating the ability of CEMs to predict species distributions under a different climate. In this framework, the results obtained with CEMs are compared with those obtained with a mechanistic model for individual species (MM). In an MM, the distribution of a species is defined by a set of functions based on knowledge of the physiology of that species. Results obtained with an MM are independent of current climate because the model parameters are not derived from the current distribution of a species. MMs are considered superior for understanding the relationship between climate and the distribution of species (Woodward & Rochefort, 1991; Malanson *et al.*, 1992; Prentice *et al.*, 1992; also see the discussion in Guisan & Zimmermann, 2000) and have been used to study the distribution of a lizard in Australia (Kearney & Porter, 2004) and effects of climate change on crop production (Rosenzweig & Parry, 1994; Hijmans, 2003). A drawback of MMs is that physiological data required to parameterize the model are not available for most species. Another problem with the use of MMs of individual species is that they tend to be based on a species eco-physiology but do not account for nonclimatic influences on species distribution such as biotic interactions or dispersal limitations (Pearson & Dawson, 2003). CEMs do not directly model such nonclimatic influences either, but they may do so indirectly if limits to species distributions caused by factors such as competition occur on an environmental gradient and are therefore correlated with environmental variables. MMs may, thus, be of limited value in comparison with CEMs for accurately predicting current distributions of species. However, MMs are uniquely suitable for understanding the effect of different climates on species distributions, when assuming universal dispersal and the absence of competition, that is, MMs can be used to evaluate the intrinsic ability of CEMs to accurately predict spatial distributions of species under different climates. In this paper, we used an MM to predict the potential distributions of 100 plant species for current conditions, and for a future (warmer) and past (colder) climate. By comparing the MM results with those obtained using four different CEMs, we evaluate the ability of each CEM to predict a species range under different climates.

Materials and methods

Climate data

We used monthly precipitation and minimum and maximum temperature data for three periods: 'current', 'future', and 'past'. For current conditions, we used the WorldClim database (Hijmans *et al*., 2005a). This dataset has a spatial resolution of approximately 1 km and was created by interpolation using a thin-plate smoothing spline of observed climate at weather stations, with latitude, longitude, and elevation as independent variables (Hutchinson, 1995, 2004). Projected future climate data were from Duffy *et al*. (2003) and Govindasamy *et al*. (2003). They ran the CCM3 global climate model (GCM) at approximately 50 km spatial resolution to simulate conditions at doubled atmospheric levels of CO_2 ($2 \times CO_2$) as compared with preindustrial conditions. To our knowledge, these data are at the highest spatial resolution currently available for projected future global climate data. Past climate data used were GCM reconstructions for the last glacial maximum (LGM; 21 000 BP). These data were generated with the ECHAM3 model (DKRZ, 1992; Lorenz *et al*., 1996), are at an approximately 312 km spatial resolution and are available at http://www.lsce.cea.fr/pmip/

For both GCMs there were also 'control runs' for the current conditions available. We calculated the difference (absolute for temperature and relative for precipitation) between the modeled current and past or future conditions and statistically downscaled these to a 1 km spatial resolution, using bilinear interpolation in Arc/Info (ESRI, Redlands, CA, USA). The projected future or past climate was then calculated from the current climate (WorldClim database) and the downscaled model differences. This approach was taken to assure consistency of the climate layers across time slices and that the downscaled climate realistically reflected the higher resolution topography.

We limited our area of study to the Americas, and projected all data to the Lambert Equal Area projection (latitude $= 0^\circ$ and longitude $= -80^\circ$) to obtain grid cells of equal area and allow for easy calculations of range sizes. We aggregated the data to cells of 10 km spatial resolution using bilinear interpolation. Mean annual temperature for this dataset was 4.8 °C for current, 0.7 °C for past, and 6.8 °C for future conditions. Mean annual precipitation was 1045 mm for current, 1128 mm for future, and 1015 mm for past conditions. Predicted past and future temperature changes were much larger at high latitudes than in the tropics. Precipitation changed in different directions in different places, and this was particularly pronounced comparing current with LGM conditions, that is, the model suggests that it was much dryer than today in some places, but much wetter in other places, resulting in similar mean precipitation across the whole study area.

In the CEMs, we used the following six bioclimatic variables (Nix, 1986): annual mean temperature, mean diurnal temperature range, mean annual temperature range, annual precipitation, precipitation seasonality (coefficient of variation), and precipitation of the driest quarter. We chose these variables because they represent general trends (means), variation (seasonality), and limiting variables (i.e. minimum and maximum temperatures). To evaluate the effect of the number of variables included on model performance, we also run the models using 19 variables: the above six and maximum temperature of the warmest month, minimum temperature of the coldest month, isothermality (monthly/annual temperature range), temperature seasonality (standard deviation across months), mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation of wettest month, precipitation of driest month, precipitation of wettest quarter, precipitation of warmest quarter, and precipitation of coldest quarter.

MM

We used the MM that is implemented in DIVA-GIS 5.1 (Hijmans *et al*., 2005b). This is a 'Plantgro' type model (Hackett & Vanclay, 1998) in which requirements for plant growth are described as plateau-shaped curves that indicate plant response (expressed as 0–1) to monthly precipitation and minimum and mean temperature. Response is zero below a minimum and above a maximum threshold, and one between a minimum and a maximum optimal value (Hijmans *et al*., 2005b; cf. Hackett, 1991; Austin, 1992). Overall response across environmental variables follows the Sprengel–Liebig Law of the Minimum (Hackett, 1991; Van der Ploeg *et al*., 1999), that is, the most limiting factor determines the overall response. Interaction between temperature and rainfall is not considered. Model scores are calculated for 24 possible growing periods, starting at the first or the 15th day of each month, the highest score is retained. The length of the growing period is specified as a number of days. For each location (grid cell) the model calculates the suitability for a species using a score from 0 (not suitable) to 100 (highly suitable). Based on comparison with known distributions of some species, we considered only areas with scores above 90 as suitable for a species.

MM parameters for 100 randomly selected plant species (out of 1710 species for which parameters were available) were taken from the ECOCROP database (FAO, 1999), which includes killing (minimum) temperature, and minimum, maximum, and range of optimal temperatures; the minimum and maximum length of the growing season; and minimum, maximum and range of optimal amount of rainfall for each species. The species included are all of economic importance, including annuals and perennials that are used for (e.g. food, fuel or fodder). We ran the MM to predict the potential distribution of the plant species, using the monthly temperature and rainfall data for current, future, and past conditions.

A similar modeling approach has been used to study the effect of climate change on species distributions by Booth *et al*. (1999) and Miles *et al*. (2004). Here, we are not concerned about the quality of the predictions made *per se*. What is important for our purpose is to have a model that provides a plausible prediction of the area that is suitable for a species, based on parameters that were not directly derived from its current known geographic distribution.

CEMs

We employed four CEMs: Bioclim, Domain, GAM, and Maxent. We chose these because they are well-known models that represent a variety of different statistical approaches. We used Bioclim (Nix, 1986; Busby, 1991) as implemented in DIVA-GIS. This model treats the environmental data values at the locations of species occurrence as multiple one-tailed percentile distributions, that is, it creates a percentile distribution for each variable so that, for example, the fifth percentile is treated the same as the 95th percentile. For each grid cell, the values of each environmental variable are assessed to determine their position in this percentile distribution. The lowest score across environmental values for a grid cell is mapped and can be 'null' (outside the observed range of values) or range from zero (low) to the theoretical maximum of 50 (very high).

In the Domain model (Carpenter *et al*., 1993), the Gower distance statistic is calculated between the values of the environmental variables of each cell and of each occurrence point. The distance between point A and grid cell B for a single climate variable k is calculated as the absolute difference between A and B divided by the range of k across all points. The Gower distance (G) is the mean of the distances for all climate variables and the Domain similarity statistic is calculated as $100 \times (1-G)$. The maximum similarity between a grid cell and any point is mapped. The maximum value is 100 (all cells in which presences occurred will have this score); a high number (e.g. >95) implies a high likelihood of the species being present. We used the Domain model as implemented in DIVA-GIS.

We used the general additive modeling (GAM) technique as implemented in GRASP version 0.4-3 (Lehmann *et al*., 2002) within the R statistical package. GAMs use nonparametric smoothers to model nonlinear trends between dependent (species presence or absence) and independent (environment) variables. We used stepwise selection of the variables and the ANOVA criterion to select the best model.

We used Maxent version 1.9.1 (available from http://www.cs.princeton.edu/~schapire/maxent/). This model is an application of a machine learning technique called 'maximum-entropy.' Maxent estimates the likelihood of a species being present by finding the distribution of maximum entropy (i.e. that is closest to uniform) subject to the constraint that the expected value of each environmental variable under this estimated distribution matches its empirical average (Phillips *et al*., 2006). Maxent uses the 'background' data of the environmental layers in the modeling process. The output of both Maxent and GAM are values between 0 (low) and 1 (high).

Model runs

For each species, we selected random points from the area predicted by the MM as currently suitable. The number of points selected was the square root of the number of cells currently deemed suitable. Sampling was done for computational efficiency and to better resemble the (sparse) data typically used in CEM. The point distributions were then used to create predictions with the CEM for current, future, and past conditions (Fig. 1). All CEMs were run using the default settings. Absence data used in GAM were the cells that were unsuitable for a species (according to the MM), but that were suitable for any of the other species, in addition to a set of random background points that covered areas currently unsuitable for all the species considered (parts of the Arctic in Canada and Greenland, and the Atacama desert in Chile).

Model evaluation

The output of CEMs are continuous values indicating the suitability of any site for the species being modeled. To transform these values to presence/absence data we determined species specific thresholds above which a species was considered present. For each model we chose the value that produced a relative range size Eqn (1) that was closest to zero (median across all species). This calibration was done for the current climate, and these thresholds were maintained throughout the modeling

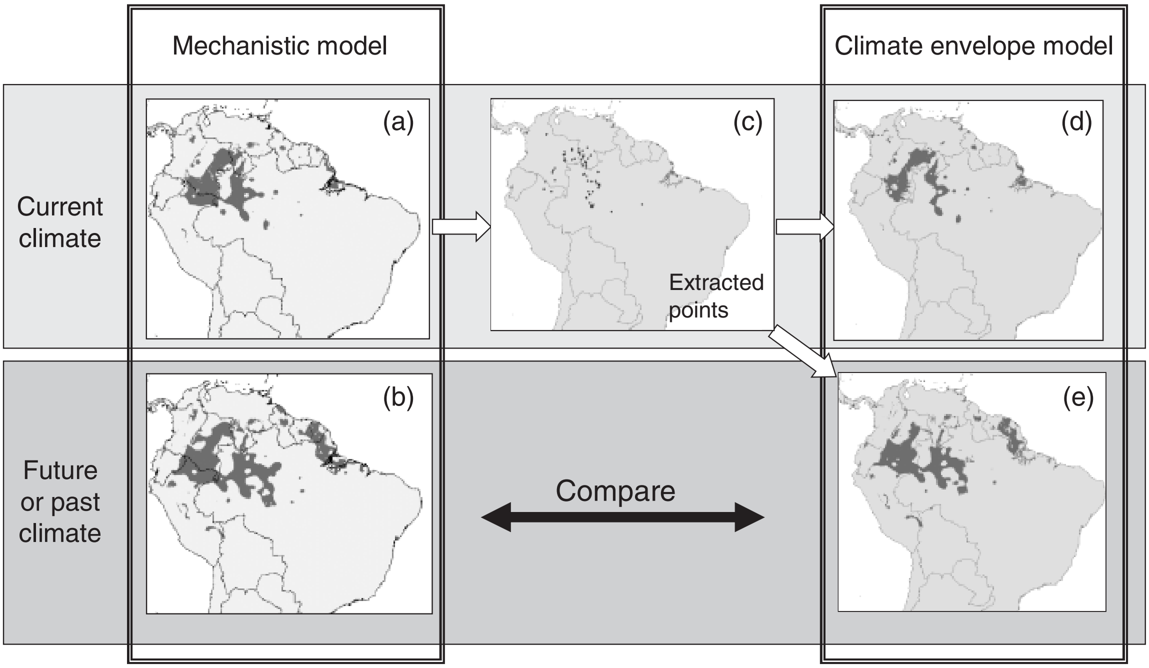

Fig. 1 Approach used to evaluate the ability of climate envelope models to predict species distributions under different climates. A mechanistic model is used to predict the potential distribution for a species under current (a) and future (or past) (b) conditions (light gray = not suitable, dark gray = suitable). Points are extracted randomly from the area deemed currently suitable for the species (c). These points are used in the climate envelope model for current (d) and future (e) conditions. The statistical model is evaluated through a comparison of (b) and (e). These maps show results for *Berrya cordifolia* (Willd.) for the Bioclim model.

exercise and experimental climate shifts, as is the general practice in climate change modeling studies. We used range size to calibrate because of the importance of range size in assessing risks of extinction (Thomas *et al*., 2004).

To evaluate how well the ranges predicted with the CEMs corresponded to those of the MM we calculated, for each species, time slice and CEM, the following four indices: relative range size [RRS; Eqn (1)], overlap index [OI; Eqn (2)], false positive rate [FPR; Eqn (3)], and false negative rate [FNR; Eqn (4)]:

$$\begin{cases} \text{if } m \leq c & \text{RRS} = c/m - 1, \\ \text{else} & \text{RRS} = -1^{*}(m/c - 1), \end{cases} \tag{1}$$

$$\text{OI} = o/m, \tag{2}$$

$$\text{FPR} = (c - o)/m, \tag{3}$$

$$\text{FNR} = (m - o)/m, \tag{4}$$

where m is (the size of) the area where the MM predicts a species to be present, c is the area where the CEM predicts presence and o is the area where they overlap, that is, both MM and CEM predict presence.

RRS compares the predicted range size of a CEM with that of the MM. It was calculated according to Eqn (1) because c/m is biased, with RRS deviating much more from 1 when $c > m$ than when $m < c$ (e.g. 1/4 vs. 4). Note, however, that a score of 3 implies that the range size predicted by the CEM was four times as big as that of the MM, and that a score of −3 implies that it was four times as small. OI measures the degree of overlap of the CEM with the MM. FPR is a measure of model overprediction ('error of commission') and FNR a measure of underprediction ('error of omission'). In our analysis, an ideal CEM would have RRS = 0, OI = 1, FPR = 0, and FNR = 0. RRS and OI were also calculated to assess the effect of climate change on the predictions made with the MM. In this case, m refers to the prediction for current conditions, and c to either future or past conditions. For each CEM and the four indices we determined the statistical significance of the differences between the predictions for the current climate and for the other climates. To this end, we used the Wilcoxon test (Mann–Whitney *U*-test), as implemented in the R package.

Results

MM

Compared with the current situation, the MMs showed considerable changes in range size for past conditions but less so for future conditions. For future conditions, RRS was −0.07 and OI was 0.54, indicating that median

Table 1 Thresholds used to assign presence or absence to grid cells for the four statistical models used, for the runs with six and 18 environmental variables

	6 variables	18 variables
Bioclim	0.07	0
Domain	93	93
GAM	0.67	0.56
Maxent	7	6

GAM, General Additive Modeling.

range size decreased slightly while the location of the ranges shifted considerably, with only half the currently suitable range also suitable under the future climate. For past conditions, RRS was −0.50 and OI was 0.14. Hence, for the last glacial maximum, modeled range sizes were considerably smaller than for the current period with past and current ranges overlapping only slightly.

Climate envelope model, current conditions

For all CEMs, we identified a threshold that produced range sizes similar to current potential ranges as modeled with the MM (RRS ≈ 0; Table 1). However, there was variation in how well CEMs reproduced the spatial extent of the ranges modeled with the MM at this threshold (Fig. 2). Maxent had the highest OI, with a median value of 0.91 (when using six environmental variables), which was marginally higher than Bioclim (0.90). OI for GAM was 0.84, while Domain had the lowest score (0.77). Maxent and Bioclim also had the lowest median FPR and FNR, again with Domain having the poorest score. Results were similar for the predictions made when using 16 variables.

Climate envelope model, past, and future conditions

The results for past and future conditions varied strongly between models (Fig. 2; Table 2). Domain substantially underpredicted species ranges, particularly for past climate conditions. It had a strong and statistically significant ($P \leq 0.01$) decrease in RRS, OI, and FPR and an increase in FNR under both past and future climates.

Bioclim performed much better than Domain across all evaluation measures but it tended to underpredict, especially when using 18 variables (Fig. 2). Bioclim stood out for a very low FPR but, in accordance with its low RRS, it had a relatively high FNR, especially when running the model with 18 climate variables. The FPR for current conditions was not significantly different from that for future or past conditions. Under future and past climates, GAM predicted range sizes that were similar to those predicted with the MM (RRS ~ 0) and its OI was better than, or comparable with that of Bioclim.

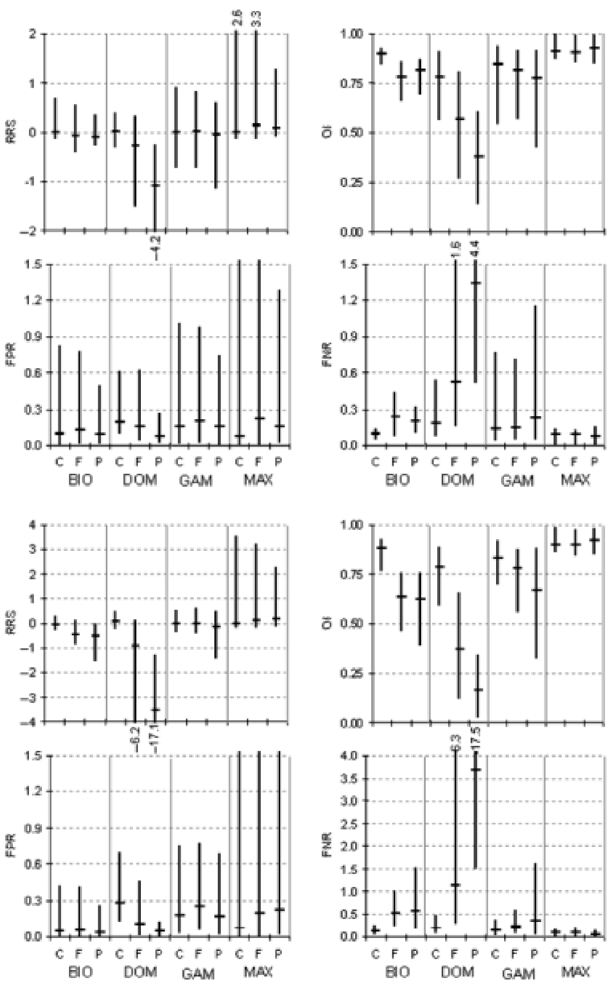

Fig. 2 Relative range size (RRS), overlap index (OI), false positive rate (FPR), and false negative rate (FNR) for a comparison between the results obtained with four climate envelope models, Bioclim (BIO), Domain (DOM), General Additive Modeling (GAM), and Maxent (MAX) and the results obtained with a mechanistic model. Six (upper panel) or 18 (lower panel) climatic variables were used in the modeling of 100 plant species for current (C), future (F; 2 × CO_2 conditions), and past (P; Last glacial maximum, 21 000 BP) conditions. Median values are shown, with a line between the 10th and 90th percentile. For legibility, some lines have been truncated, but in those cases the values of the 10th or 90th percentile are provided at the point of truncation.

RRS for Maxent was close to zero, but not as close as for GAM. Maxent was the only model that had a median RRS>0, that is, it predicted larger range sizes than the MM. The relatively high RRS is accompanied by a relatively high OI (i.e. most of the areas predicted suitable are correctly classified). A high RRS could come at the expense of a high FPR. However, the median FPR for Maxent was not always higher than for

Table 2 Statistical significance of differences between performance under future and past climate conditions of four climate envelope models relative to their performance under current conditions

	Bioclim		Domain		GAM		Maxent	
	Future	Past	Future	Past	Future	Past	Future	Past
6 variables								
RRS	<0.01	<0.01	<0.01	<0.01	0.50	0.19	0.05	0.01
OI	<0.01	<0.01	<0.01	<0.01	0.27	0.01	0.31	0.25
FPR	0.34	0.80	0.01	<0.01	0.12	0.92	0.01	<0.01
FNR	<0.01	<0.01	<0.01	<0.01	0.64	0.01	0.85	0.15
18 variables								
RRS	<0.01	<0.01	<0.01	<0.01	0.61	<0.01	0.25	<0.01
OI	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.32	0.22
FPR	0.68	0.13	<0.01	<0.01	0.16	0.60	0.01	<0.01
FNR	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	0.85	0.02

Calculated using the Wilcoxon test (=Mann–Whitney *U*-test) for four indices (see text): relative range size (RRS), overlap index (OI), false positive rate (FPR), and false negative rate (FNR), with $n = 100$ plant species, and for models run with six or 18 environmental variables.
GAM, General Additive Modeling.

GAM, albeit that it was highly variable for Maxent, indicating that while its performance is good overall, predictions for a few species may be quite poor.

For Domain and Bioclim there was a clear effect of the number of environmental variables used on RRS and OI with the results becoming worse when more variables were used (Fig. 2). The results obtained with GAM were less affected, but GAM performed better when only six instead of 18 climatic variables were used (Table 2). For Maxent the results obtained with six and with 18 variables were similar.

Discussion

The output of the MMs allowed us to evaluate the ability of CEMs to predict species distributions across time (climate regimes), independently of nonclimatic factors that influence true species distributions and that can make model results difficult to evaluate. MMs predicted marked range reductions for the colder climate and shifted locations for both colder and warmer climates than today. We found considerable variation between CEMs in their ability to reproduce these predictions, as was to be expected given previously reported variation in such predictions (Thuiller, 2003, 2004; Pearson *et al.*, 2006). Maxent and GAM provided reasonably good estimates of potential range shifts with climate change. Domain strongly underestimated range sizes. This model should not be used to predict the effects of climate change on species distributions. Bioclim performed better than Domain, but not as well as the other two models, because Bioclim systematically underpredicts range sizes.

Of the four climate envelope modeling methods examined here, GAM might be the most appropriate if the objective is to predict the likelihood of species extinction because it predicted relative range size most faithfully. Maxent had high spatial concordance with MMs (high OI) and low false negative rates, which came at a cost of a slight increase in RRS (>1), relative to GAM. For many applications, the benefit of having a more accurate spatial representation of species distribution patterns under different climates would offset the cost of an increase of RRS. However, Maxent did show high variation in RRS and FPR, with occasional very strong overprediction, something that GAM and particularly Bioclim were much less prone to. Bioclim can be used as a conservative approach, for example, in the context of reserve planning. It will likely underestimate future ranges, but there is a high probability that areas identified as suitable for a species will be correctly identified.

Examining the mathematical properties of the climate envelope modeling methods can help explain the differences in their performance. Domain uses the Gower distance metric to calculate suitability for a grid cell by calculating a mean (over climate variables) weighted distance of a grid cell to the nearest (in climate space) occurrence point. All occurrence points are treated separately and, unlike in the other models, there is no generalization (creation of response functions). With a change in climate, the average environmental distance of the sites (grid cells) to the occurrence points is much more likely to increase than to decrease. In other words, Domain is probably very sensitive to the occurrence of new combinations of the environmental variables and this negatively affects its ability to predict a species'

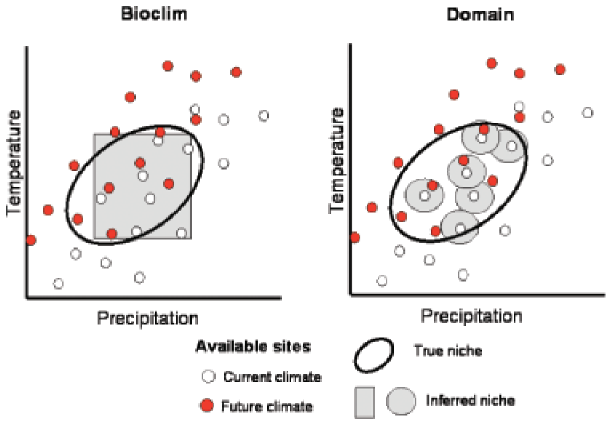

Fig. 3 Schematic description of predicting the distribution of a species under different climates using two climate envelope models, Bioclim, and Domain. There are 15 sites, with different climates in the two time periods. The true requirements of the species are constant and indicated with an ellipsoid. The inferred requirements do not fully overlap with the true requirements because there are insufficient sites where the species has been observed and/or because parts of the true niche are currently not present on the landscape, and because the model methods are imperfect. Under future conditions, model performance is diminished because some sites are incorrectly classified as not having the species (false negatives).

response to climate change. Bioclim uses independent percentile distributions and is, therefore, less likely to be very sensitive to the occurrence of new combinations of environmental variables. However, if one or more environmental variables are outside what was observed in the current climate, even if this is not truly a limiting factor, then Bioclim will underpredict (Fig. 3). GAM and Maxent both use presence and absence (or random background) data. This likely makes them able to correctly identify as suitable at least some of the 'new' environmental space if the conditions are closer to the conditions under which the species is currently present than to the conditions under which it is absent. Accordingly, Maxent and GAM both seemed to be able to predict species distributions under novel combinations of climate space.

The number of environmental variables used for modeling strongly influenced the results with both Domain and Bioclim. This contrasts with the results of Beaumont *et al*. (2005), who found that Bioclim was insensitive to the number of variables used. The extent to which the number of variables influences the results should be related to how correlated they are, and perhaps that explains the differences between our results and those of Beaumont *et al*. (2005). GAM and Maxent were much less influenced by the number of variables used than either Bioclim or Domain. GAM and Maxent use variable selection (stepwise variable selection in the GRASP implementation of GAM) or weighting and should thus be inherently less sensitive to possible model overfitting. In some cases, Maxent may have removed too many variables, leading it to occasionally strongly overpredict range sizes.

We can only speculate whether the results reported by Thomas *et al*. (2004) are affected by the modeling artifacts uncovered here, but it certainly is a possibility that some of the modeling approach used in that study suffered from this problem. Of the nine data sets considered by Thomas *et al*., two had been analyzed with Bioclim, and one with an approach that appears to combine aspects of Domain and Bioclim. For example, Bioclim was used to model the effect of climate change on Australian butterflies. This work was reported extensively by Beaumont *et al*. (2005) who used Bioclim to model the distribution of 25 species in various ways and found that in 91% of 300 cases the species declined in range. Our findings suggest that these results might be an artifact of the Bioclim model, and that this may have biased the results obtained by Thomas *et al*. (2004).

Our results also suggest that that some CEMs can indeed be useful to predict the effect of climate change on species distributions. CEMs were also reasonably good at predicting the distributions of British birds under recent climate change (Araújo *et al*., 2005a, b); and were able to predict changes in range sizes that are similar to those predicted from molecular data (Ruegg *et al*., 2006). While these results are encouraging, several caveats need consideration. In our experimental design, we purposefully eliminated nonclimatic effects on species distributions, a basic assumption that is always made when using CEMs to assess the effect of climate change (Pearson & Dawson, 2003). In reality, species distributions may be limited by both biotic and abiotic factors such as species interactions and dispersal limitation (Davis *et al*., 1998; Kearney & Porter, 2004; Araújo & Pearson, 2005; Guisan & Thuiller, 2005), some of which are anthropogenic (La Sorte, 2006). Further, most data used for CEMs are from natural history collections and may have inaccurate georeferences (Wieczorek *et al*., 2004), and are biased in geographic space (Hijmans *et al*., 2000) which can lead to biased distributions in environmental space (Kadmon *et al*., 2004). While significant progress in increasing the accuracy of CEMs has been made, model accuracy is still low for some regions and species (Elith *et al*., 2006). Moreover, the best models for predicting current distributions might 'overfit' the data and such loss of generality could make them less suitable to predict future distributions (Randin *et al*., 2006).

In conclusion, we believe that progress in using CEMs to predict the effect of climate change on species distributions can be made through a number of complementary approaches, including (1) improving data and modeling methods for predicting current distributions (Graham *et al*., 2004; Guisan & Thuiller, 2005; Elith *et al*., 2006); (2) evaluating the ability of CEMs to provide accurate estimates of the effect of climate change by comparing them with mechanistic approaches, as was done in this paper; (3) increasing understanding of the drivers of species distributions, and the extent to which these are directly related to individual climatic variables (Kearney & Porter, 2004; Gavin & Hu, 2006), and how responses to climate change are affected by genetic variability (Harte *et al*., 2004); (4) comparing predicted past distributions with insights from fossil, pollen, and molecular data (Hugall *et al*., 2002; Martínez-Meyer *et al*., 2004; Ruegg *et al*., 2006); and (5) integrating CEM and mechanistic modeling approaches (Midgley & Thuiller, 2005).

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