

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

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4 Robert J. Hijmans¹ and Catherine H. Graham²
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8 ¹ Museum of Vertebrate Zoology, University of California, 3101 Valley Life Sciences
9 Building, Berkeley, CA, USA. Current address: International Rice Research Institute,
10 Los Baños, Philippines.

11 ² Department of Ecology and Evolution, Stony Brook University, 636 Life Science Building,
12 Stony Brook, NY, USA.
13
14

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20 **Corresponding author:**

21 Robert J. Hijmans
22 International Rice Research Institute
23 Los Baños, Philippines
24 r.hijmans@cgiar.org
25

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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 pre-industrial CO₂ 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.

1 Introduction

2 A number of species have been affected by recent climatic change, with changes in
3 phenology and ranges expanding towards higher latitudes and altitudes (e.g. Root *et al.* 2003;
4 Parmesan and Yohe 2003). Understanding how species will respond to projected future
5 climate change is of fundamental importance for effective management and conservation of
6 biodiversity (Hannah *et al.* 2002). Likewise, insight into the distributions of species during
7 past climates can help to understand current patterns of species distributions and genetic
8 variation (Hugall *et al.* 2002; Peterson *et al.* 2004; Graham *et al.* 2006; Rugg *et al.* 2006).
9 Predicting species ranges for different climates is commonly done with ‘climate envelope
10 models’ (CEMs) that use the current geographic distribution of a species to infer its
11 environmental requirements. Based on these requirements, a species' geographic distribution
12 for the current, or for past or future climates is predicted. A recent compilation of such
13 studies on the effect of projected climate change indicates that an alarming number of species
14 may lose a large part of their range and become ‘committed to extinction’ (Thomas *et al.*
15 2004).

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

25 A persistent problem with CEMs is the difficulty in evaluating predicted distributions
26 under different climates (i.e. reconstructions of past climates or projections of future
27 climates). Whereas predictions under current circumstances can be tested using independent
28 model training and testing datasets (Fielding and Bell 1997), such a direct assessment can not
29 be done for future climates, for which there are no observed data. Using the fossil record,
30 such tests are in principle possible for past climates (Martínez-Meyer *et al.* 2004), but the
31 number of sites from which fossils of a species are known for a given time period is often

1 very small, and the available climate reconstructions are coarse and uncertain. Araújo *et al.*
2 (2005a, b) used recent changes in the distribution of breeding birds in Britain and found
3 reasonable agreement between observed and predicted changes over a period of 20 years.
4 Such studies are useful but may be hampered by the confounding effect of changes in
5 species' ranges for reasons unrelated to climate change (e.g. anthropogenic land cover
6 change). Finally, some support for the use of CEMs for climate change studies can be drawn
7 from successes in predicting a species range from data from one continent to another, as has
8 been done for introduced invasive species (Peterson 2003; Thuiller *et al.* 2005).

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

23 Here, we present a new framework for evaluating the ability of CEMs to predict
24 species distributions under a different climate. In this framework, the results obtained with
25 CEMs are compared with those obtained with a mechanistic model for individual species
26 (MM). In an MM, the distribution of a species is defined by a set of functions based on
27 knowledge of the physiology of that species. Results obtained with an MM are independent
28 of current climate because the model parameters are not derived from the current distribution
29 of a species. MMs are considered superior for understanding the relationship between climate
30 and the distribution of species (Woodward and Rochefort 1991; Prentice *et al.* 1992
31 Malanson *et al.* 1992; also see the discussion in Guisan and Zimmermann, 2000) and have

1 been used to study the distribution of a lizard in Australia (Kearney and Porter 2004) and
2 effects of climate change on crop production (Rosenzweig and Parry 1994; Hijmans 2003). A
3 drawback of MMs is that physiological data required to parameterize the model are not
4 available for most species. Another problem with the use of MMs of individual species is that
5 they tend to be based on a species eco-physiology but do not account for non-climatic
6 influences on species distribution such as biotic interactions or dispersal limitations (Pearson
7 and Dawson 2003). CEMs do not directly model such non-climatic influences either, but they
8 may do so indirectly if limits to species distributions caused by factors such as competition
9 occur on an environmental gradient and are therefore correlated with environmental
10 variables. MMs may, thus, be of limited value in comparison with CEMs for accurately
11 predicting current distributions of species. However, MMs are uniquely suitable for
12 understanding the effect of different climates on species distributions, when assuming
13 universal dispersal and the absence of competition, that is, MMs can be used to evaluate the
14 intrinsic ability of CEMs to accurately predict spatial distributions of species under different
15 climates. In this paper, we used an MM to predict the potential distributions of 100 plant
16 species for current conditions, and for a future (warmer) and past (colder) climate. By
17 comparing the MM results with those obtained using four different CEMs, we evaluate the
18 ability of each CEM to predict a species range under different climates.

1 Materials and methods

3 *Climate data*

4 We used monthly precipitation and minimum and maximum temperature data for
5 three periods: ‘current’, ‘future’, and ‘past’. For current conditions, we used the WorldClim
6 database (Hijmans *et al.* 2005a). This dataset has a spatial resolution of approximately. 1 km
7 and was created by interpolation using a thin-plate smoothing spline of observed climate at
8 weather stations, with latitude, longitude and elevation as independent variables (Hutchinson
9 1995, 2004). Projected future climate data were from Duffy *et al.* (2003) and Govindasamy
10 *et al.* (2003). They ran the CCM3 global climate model (GCM) at approximately 50 km
11 spatial resolution to simulate conditions at doubled atmospheric levels of CO₂ (2×CO₂) as
12 compared to pre-industrial conditions. To our knowledge, these data are at the highest spatial
13 resolution currently available for projected future global climate data. Past climate data used
14 were GCM reconstructions for the last glacial maximum (LGM; 21,000 BP). These data were
15 generated with the ECHAM3 model (DKRZ 1992; Lorenz *et al.* 1996), are at a
16 approximately 312 km spatial resolution and are available at <http://www-lsce.cea.fr/pmip/>.

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

25 We limited our area of study to the Americas, and projected all data to the Lambert
26 Equal Area projection (latitude = 0° and longitude = -80°) to obtain grid cells of equal area
27 and allow for easy calculations of range sizes. We aggregated the data to cells of 10 km
28 spatial resolution using bilinear interpolation. Mean annual temperature for this dataset was
29 4.8°C for current, 0.7°C for past and 6.8°C for future conditions. Mean annual precipitation
30 was 1045 mm for current, 1128 mm for future and 1015 mm for past conditions. Predicted
31 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.

Mechanistic model

We used the mechanistic model (MM) that is implemented in DIVA-GIS 5.1 (Hijmans *et al.* 2005b). This is a 'Plantgro' type model (Hackett and Vanclay 1998) in which requirements for plant growth are described as plateau-shaped curves that indicate plant response (expressed as 0 to 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 (Van der Ploeg *et al.* 1999; Hackett 1991), 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

1 suitability for a species using a score from 0 (not suitable) to 100 (highly suitable). Based on
2 comparison with known distributions of some species, we considered only areas with scores
3 above 90 as suitable for a species.

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

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

20 *Climate envelope models*

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

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

10 We used the general additive modeling (GAM) technique as implemented in GRASP
11 version 0.4-3 (Lehmann *et al.* 2002) within the R statistical package. GAMs use non-
12 parametric smoothers to model non-linear trends between dependent (species presence or
13 absence) and independent (environment) variables. We used step-wise selection of the
14 variables and the ANOVA criterion to select the best model.

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

23 24 *Model runs*

25 For each species, we selected random points from the area predicted by the MM as
26 currently suitable. The number of points selected was the square root of the number of cells
27 currently deemed suitable. Sampling was done for computational efficiency and to better
28 resemble the (sparse) data typically used in CEM. The point distributions were then used to
29 create predictions with the CEM for current, future and past conditions (Figure 1). All CEMs
30 were run using the default settings. Absence data used in GAM were the cells that were
31 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 (Formula 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 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*; Formula 1), overlap index (*OI*; Formula 2), false positive rate (*FPR*; Formula 3), and false negative rate (*FNR*; Formula 4).

$$\begin{cases} \text{if } m = c & RRS = c / m - 1 \\ \text{else} & RRS = -1 * (m / c - 1) \end{cases} \quad \text{Formula 1}$$

$$OI = o / m \quad \text{Formula 2}$$

$$FPR = (c - o) / m \quad \text{Formula 3}$$

$$FNR = (m - o) / m \quad \text{Formula 4}$$

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.

1 *RRS* compares the predicted range size of a CEM with that of the MM. It was calculated
2 according to formula 1 because c / m is biased, with *RRS* deviating much more from 1 when
3 $c > m$ than when $m < c$ (e.g. $\frac{1}{4}$ vs. 4). Note, however, that a score of 3 implies that the range
4 size predicted by the CEM was 4 times as big as that of the MM, and that a score of - 3
5 implies that it was 4 times as small. *OI* measures the degree of overlap of the CEM with the
6 MM. *FPR* is a measure of model over-prediction ('error of commission') and *FNR* a measure
7 of under-prediction ('error of omission'). In our analysis, an ideal CEM would have $RRS = 0$,
8 $OI = 1$, $FPR = 0$ and $FNR = 0$. *RRS* and *OI* were also calculated to assess the effect of climate
9 change on the predictions made with the MM. In this case, m refers to the prediction for
10 current conditions, and c to either future or past conditions. For each CEM and the four
11 indices we determined the statistical significance of the differences between the predictions
12 for the current climate and for the other climates. To this end, we used the Wilcoxon test
13 (Mann-Whitney U test), as implemented in the R package.

1 Results

3 *Mechanistic model*

4 Compared with the current situation, the MMs showed considerable changes in range
5 size for past conditions but less so for future conditions. For future conditions, *RRS* was
6 -0.07 and *OI* was 0.54, indicating that median range size decreased slightly while the
7 location of the ranges shifted considerably, with only half the currently suitable range also
8 suitable under the future climate. For past conditions, *RRS* was -0.50 and *OI* was 0.14.
9 Hence, for the last glacial maximum, modeled range sizes were considerably smaller than for
10 the current period with past and current ranges overlapping only slightly.

12 *Climate envelope model, current conditions*

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

22 *Climate envelope model, past and future conditions*

23 The results for past and future conditions varied strongly between models (Figure 2;
24 Table 2). Domain substantially under-predicted species ranges, particularly for past climate
25 conditions. It had a strong and statistically significant ($P = 0.01$) decrease in *RRS*, *OI* and
26 *FPR* and an increase in *FNR* under both past and future climates.

27 Bioclim performed much better than Domain across all evaluation measures but it
28 tended to under-predict, especially when using 18 variables (Figure 2). Bioclim stood out for
29 a very low *FPR* but, in accordance with its low *RRS*, it had a relatively high *FNR*, especially
30 when running the model with 18 climate variables. The *FPR* for current conditions was not
31 significantly different from that for future or past conditions. Under future and past climates,

1 GAM predicted range sizes that were similar to those predicted with the MM ($RRS \sim 0$) and
2 its OI was better than, or comparable with that of Bioclim.

3 RRS for Maxent was close to zero, but not as close as for GAM. Maxent was the only
4 model that had a median $RRS > 0$, that is, that predicted larger range sizes than the MM. The
5 relatively high RRS is accompanied by a relatively high OI , (i.e. most of the areas predicted
6 suitable are correctly classified). A high RRS could come at the expense of a high FPR .
7 However, the median FPR for Maxent was not always higher than for GAM, albeit that it
8 was highly variable for Maxent, indicating that while its performance is good overall,
9 predictions for a few species may be quite poor.

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

1 Discussion

2 The output of the mechanistic models allowed us to evaluate the ability of CEMs to
3 predict species distributions across time (climate regimes), independently of non-climatic
4 factors that influence true species distributions and that can make model results difficult to
5 evaluate. MMs predicted marked range reductions for the colder climate and shifted locations
6 for both colder and warmer climates than today. We found considerable variation between
7 CEMs in their ability to reproduce these predictions, as was to be expected given previously
8 reported variation in such predictions (Thuiller 2003, 2004; Pearson *et al.*, in press).

9 Maxent and GAM provided reasonably good estimates of potential range shifts with
10 climate change. Domain strongly underestimated range sizes. This model should not be used
11 to predict the effects of climate change on species distributions. Bioclim performed better
12 than Domain, but not as well as the other two models, because Bioclim systematically under-
13 predicts range sizes.

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

25 Examining the mathematical properties of the climate envelope modeling methods
26 can help explain the differences in their performance. Domain uses the Gower distance
27 metric to calculate suitability for a grid cell by calculating a mean (over climate variables)
28 weighted distance of a grid cell to the nearest (in climate space) occurrence point. All
29 occurrence points are treated separately and, unlike in the other models, there is no
30 generalization (creation of response functions). With a change in climate, the average
31 environmental distance of the sites (grid cells) to the occurrence points is much more likely

1 to increase than to decrease. In other words, Domain is probably very sensitive to the
2 occurrence of new combinations of the environmental variables and this negatively affects its
3 ability to predict a species' response to climate change. Bioclim uses independent percentile
4 distributions and is, therefore, less likely to be very sensitive to the occurrence of new
5 combinations of environmental variables. However, if one or more environmental variables
6 are outside what was observed in the current climate, even if this is not truly a limiting factor,
7 then Bioclim will under-predict (Figure 3). GAM and Maxent both use presence and absence
8 (or random background) data. This likely makes them able to correctly identify as suitable at
9 least some of the 'new' environmental space if the conditions are closer to the conditions
10 under which the species is currently present than to the conditions under which it is absent.
11 Accordingly, Maxent and GAM both seemed to be able to predict species distributions under
12 novel combinations of climate space.

13 The number of environmental variables used for modeling strongly influenced the
14 results with both Domain and Bioclim. This contrasts with the results of Beaumont *et al.*
15 (2005), who found that Bioclim was insensitive to the number of variables used. The extent
16 to which the number of variables influences the results should be related to how correlated
17 they are, and perhaps that explains the differences between our results and those of
18 Beaumont *et al.* (2005). GAM and Maxent were much less influenced by the number of
19 variables used than either Bioclim or Domain. GAM and Maxent use variable selection
20 (stepwise variable selection in the GRASP implementation of GAM) or weighting and should
21 thus be inherently less sensitive to possible model overfitting. In some cases, Maxent may
22 have removed too many variables, leading it to occasionally strongly over-predict range
23 sizes.

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

1 Our findings suggest that these results might be an artifact of the Bioclim model, and that this
2 may have biased the results obtained by Thomas *et al.* (2004).

3 Our results also suggest that that some CEMs can indeed be useful to predict the
4 effect of climate change on species distributions. CEMs were also reasonably good at
5 predicting the distributions of British birds under recent climate change (Araújo *et al.* a, b
6 2005); and were able to predict changes in range sizes that are similar to those predicted from
7 molecular data (Ruegg *et al.* 2006). While these results are encouraging, several caveats need
8 consideration. In our experimental design, we purposefully eliminated non-climatic effects
9 on species distributions, a basic assumption that is always made when using CEMs to assess
10 the effect of climate change (Pearson and Dawson 2003). In reality, species distributions may
11 be limited by both biotic and abiotic factors such as species interactions and dispersal
12 limitation (Davis *et al.* 1998; Kearney and Porter 2004; Araújo and Pearson 2005; Guisan
13 and Thuiller 2005), some of which are anthropogenic (La Sorte 2006). Further, most data
14 used for CEMs are from natural history collections and may have inaccurate georeferences
15 (Wieczorek *et al.* 2004), and are biased in geographic space (Hijmans *et al.* 2001) which can
16 lead to biased distributions in environmental space (Kadmon *et al.* 2004). While significant
17 progress in increasing the accuracy of CEMs has been made, model accuracy is still low for
18 some regions and species (Elith *et al.* 2006). Moreover, the best models for predicting current
19 distributions might 'overfit' the data and such loss of generality could make them less suitable
20 to predict future distributions (Randin *et al.*, in press).

21 In conclusion, we believe that progress in using CEMs to predict the effect of climate
22 change on species distributions can be made through a number of complementary
23 approaches, including (1) improving data and modeling methods for predicting current
24 distributions (Graham *et al.* 2004; Guisan & Thuiller 2005; Elith *et al.* 2006); (2) evaluating
25 the ability of CEMs to provide accurate estimates of the effect of climate change by
26 comparing them to mechanistic approaches, as was done in this paper; (3) increasing
27 understanding of the drivers of species distributions, and the extent to which these are
28 directly related to individual climatic variables (Kearney and Porter 2004; Gavin and Hu
29 2006), and how responses to climate change are affected by genetic variability (Harte *et al.*
30 2004); (4) comparing predicted past distributions with insights from fossil, pollen, and
31 molecular data (Hugall *et al.* 2002; Martínez-Meyer *et al.* 2004; Ruegg *et al.* 2006); and (5)

- 1 integrating CEM and mechanistic modeling approaches (Midgley and Thuiller 2005; Thuiller
- 2 *et al.* 2006).

References

- Araújo MB, Pearson RG, Thuiller W, Erhard M (2005a) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Araújo MB, Whittaker, RJ, Ladle, RJ, Erhard M (2005b) Reducing uncertainty in projects of extinction risk from climate change. *Global Ecology and Biogeography*, **14**, 529–538.
- Araújo MB, Pearson RG (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.
- Austin MP (1992) Modelling the environmental niche of plants: implications for plant community response to elevated CO₂ levels. *Australian Journal of Botany*, **40**, 615–30.
- Beaumont LJ, Hughes L, Poulsen M (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological modelling*, **186**, 250–269.
- Booth TH, Nghia NH, Kirschbaum MUF, Hackett C, Jovanovic T (1999) Assessing Possible Impacts of Climate Change on Species Important for Forestry in Vietnam. *Climatic Change*, **41**, 1573–1480
- Busby JR (1991) Bioclim—a bioclimatic analysis and prediction system. *Plant Protection Quarterly*, **6**, 8–9.
- Carpenter G, Gillison AN, Winter J (1993) Domain: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity Conservation*, **2**, 667–680.
- Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- DKRZ (Deutsches Klimarechenzentrum Modellbetreuungsgruppe) (1992) *The ECHAM3 atmospheric general circulation model*. DKRZ Technical Report 6. Deutsches Klimarechenzentrum, Hamburg, 184 p.
- Duffy PB, Govindasamy B, Lorio JP, *et al.* (2003) High resolution simulations of global climate, Part 1: present climate. *Climate Dynamics*, **21**, 371–390.
- Elith J, Graham CH, Anderson RP, *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- FAO (Food and Agriculture Organization of the United Nations) (1999) *ECOCROP 1 & 2. The crop environmental requirements database & the crop environmental response database*. FAO Land and Water Digital Media Series 4, CD-ROM, FAO, Rome.
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Gavin DG, Hu FS (2006) Spatial variation of climatic and non-climatic controls on species distribution: the range limit of *Tsuga heterophylla*. *Journal of Biogeography*, **33**, 1384–1396.
- Govindasamy B, Duffy PB, Coquard J (2003) High-resolution simulations of global climate, part 2: effects of increased greenhouse gases. *Climate Dynamics*, **21**, 391–404.
- Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution*, **19**, 497–503.
- Graham CH, Moritz C, Williams SE (2006) Habitat history improves prediction of biodiversity in a rainforest fauna. *Proceedings of the National Academy of Sciences*, **103**, 632–636.

- 1 Guisan A, Thuiller W (2005) Predicting species distributions: offering more than simple
2 habitat models. *Ecology Letters*, **8**, 993-1003.
- 3 Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology.
4 *Ecological Modelling*, **135**, 147-186.
- 5 Hackett C (1991) *Plantgro: a software package for the coarse prediction of plant growth*.
6 Melbourne, CSIRO.
- 7 Hackett C, Vanclay JK (1998) Mobilizing expert knowledge of tree growth with the
8 PLANTGRO and INFER systems. *Ecological Modelling*, **106**, 233-246.
- 9 Hannah L, Midgley GF, Millar D (2002) Climate change-integrated conservation strategies
10 *Global Ecology & Biogeography*, **11**, 485-495.
- 11 Harte J, Ostling A, Green JL, Kinzig A (2004) Climate change and extinction risk. *Nature*,
12 **430**, 36.
- 13 Hijmans RJ (2003) The effect of climate change on global potato production. *American*
14 *Journal of Potato Research*, **80**, 271-280.
- 15 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005a) Very high resolution
16 interpolated global terrestrial climate surfaces. *International Journal of Climatology*,
17 **25**, 1965-1978.
- 18 Hijmans RJ, Guarino L, Bussink C, Barrantes I, Rojas, E (2005b) *DIVA-GIS, version 5*.
19 *Manual*. Available at <http://www.diva-gis.org/>.
- 20 Hugall A, Moritz C, Moussalli A, Stanislav J (2002) Reconciling paleodistribution models and
21 comparative phylogeography in the wet tropics rainforest land snail *Gnarosophia*
22 *bellendenkerensis*. *Proceedings of the National Academy of Sciences USA*, **99**, 6112-
23 6117.
- 24 Hutchinson MF (1995) Interpolating mean rainfall using thin plate smoothing splines.
25 *International Journal of Geographical Information Systems*, **9**, 385-403.
- 26 Hutchinson MF (2004) *Anusplin version 4.3*. Centre for Resource and Environmental
27 Studies. The Australian National University, Canberra.
- 28 Kadmon R, Farber O, Danin A (2004) Effect of roadside bias on the accuracy of predictive
29 maps produced by bioclimatic models. *Ecological Applications*, **14**, 401-413.
- 30 Kearney M, Porter WP (2004) Mapping the fundamental niche: physiology, climate, and the
31 distribution of a nocturnal lizard. *Ecology* **85**, 3119-3131.
- 32 La Sorte F (2006) Geographical expansion and increased prevalence of common species in
33 avian assemblages: implications for large-scale patterns of species richness. *Journal of*
34 *Biogeography*, **33**, 1183-1191
- 35 Lehmann A, Overton JMC, Leathwick JR (2002) GRASP: Generalized Regression Analysis
36 and Spatial Predictions. *Ecological Modelling*, **157**, 189-207.
- 37 Lorenz S, Grieger B, Helbig P, Herterich K (1996) Investigating the sensitivity of the
38 Atmospheric General Circulation Model ECHAM 3 to paleoclimatic boundary
39 conditions. *Geologische Rundschau*, **85**, 513-524.
- 40 Malanson GP, Westman WE, Yan Y-L (1992) Realized versus fundamental niche functions
41 in a model of chaparral response to climatic change. *Ecological Modelling*, **64**, 261-
42 277.
- 43 Martínez-Meyer E, Peterson AT, Hargrove WW (2004) Ecological niches as stable
44 distributional constraints on mammal species, with implications for Pleistocene
45 extinctions and climate change projections for biodiversity. *Global Ecology and*
46 *Biogeography* **13**, 305-314.

- 1 Midgley GF, Thuiller W (2005) Global environmental change and the uncertain fate of
2 biodiversity. *New Phytologist*, **167**, 638-641.
- 3 Miles L, Grainger A, Phillips O (2004) The impact of global climate change on tropical
4 forest biodiversity in Amazonia. *Global Ecology and Biogeography*, **13**, 553-565
- 5 Nix HA (1986) A biogeographic analysis of Australian elapid snakes. In: *Atlas of Elapid*
6 *Snakes of Australia*. Australian Flora and Fauna Series No. 7 (ed. R. Longmore). pp. 4-
7 15. Australian Government Publishing Service, Canberra.
- 8 Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts
9 across natural systems. *Nature*, **421**, 37-42.
- 10 Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution
11 of species: are bioclimatic envelope models useful? *Global Ecology and Biogeography*,
12 **12**, 361-371.
- 13 Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L,
14 Segurado P, Dawson TE, Lees DC (in press) Model-based uncertainty in species' range
15 prediction. *Journal of Biogeography*.
- 16 Peterson AT (2003) Predicting the geography of species' invasions via ecological niche
17 modeling. *The Quarterly Review of Biology*, **78**, 419-433.
- 18 Peterson AT, Martinez-Meyer E, González-Salazar C (2004) Reconstructing the Pleistocene
19 geography of the Aphelocoma jays (Corvidae). *Diversity and Distributions*, **10**, 237-
20 246.
- 21 Phillips SJ, Anderson R, Schapire RE (2006) Maximum entropy modeling of species
22 geographic distributions. *Ecological Modelling*, **190**, 231-259.
- 23 Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A
24 global biome model based on plant physiology and dominance, soil properties and
25 climate. *Journal of Biogeography*, **19**, 117-134.
- 26 Randin CF, Dirnböck T, Dullinger S, Zimmermann NE, Zappa M, Guisan A (in press) Are
27 niche-based species distribution models transferable in space? *Journal of Biogeography*
- 28 Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) 'Fingerprints'
29 of global warming on animals and plants. *Nature*, **421**, 57-60.
- 30 Rosenzweig C, Parry ML (1994) Potential impact of climate change on world food supply.
31 *Nature*, **367**, 133-138.
- 32 Ruegg K, Hijmans RJ, Moritz C (2006) Climate change and the origin of migratory pathways
33 in the Swainson's Thrush, *Catharus ustulatus*. *Journal of Biogeography*, **33**, 1172-
34 1182.
- 35 Theurillat J-P, Guisan A (2001) Potential impact of climate change on vegetation in the
36 european alps: a review. *Climatic Change*, **50**, 77-109.
- 37 Thomas CD, Cameron A, Green RE, *et al.* (2004) Extinction risk from climate change.
38 *Nature*, **427**, 145-148.
- 39 Thuiller W (2003) BIOMOD – optimizing predictions of species distributions and projecting
40 potential future shifts under global change. *Global Change Biology*, **9**, 1353-1362.
- 41 Thuiller W (2004) Patterns and uncertainties of species' range shifts under climate change.
42 *Global Change Biology*, **10**, 2020-2027.
- 43 Thuiller W, Araújo MB, Pearson RG, Whittaker RJ, Brotons L, Lavorel S (2004)
44 Biodiversity conservation - uncertainty in predictions of extinction risk. *Nature*, **430**,
45 36.

- 1 Thuiller W, Richardson DM, Pyšek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-
2 based modelling as a tool for predicting the risk of alien plant invasions at a global
3 scale. *Global Change Biology*, **11**, 2234–2250.
- 4 Van der Ploeg RR, Böhm W, Kirkham, MB (1999) On the origin of the theory of mineral
5 nutrition of plants and the law of the minimum. *Soil Science Society of America*
6 *Journal*, **63**, 1055-1062.
- 7 Williams SE, Bolitho EE, Fox S (2003) Climate change in Australian tropical rainforests: an
8 impending environmental catastrophe. *Proceedings of the Royal Society of London,*
9 *Biological Sciences*, **270**, 1887-1892.
- 10 Wieczorek JR, Guo Q, Hijmans RJ (2004) The point-radius method for georeferencing point
11 localities and calculating associated uncertainty. *International Journal of Geographic*
12 *Information Science*, **18**, 745–767
- 13 Woodward FI, Rochefort I (1991) Sensitivity analysis of vegetation diversity to
14 environmental change. *Global Ecology and Biogeography Letters*, **1**, 7–23.

1 Table 1. Thresholds used to assign presence or absence to grid cells for the four statistical
 2 models used, for the runs with 6 and 18 environmental variables.

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

3

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. 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 6 or 18 environmental variables.

	Bioclim		Domain		GAM		Maxent	
	future	past	future	past	future	past	future	past
<i>6 variables</i>								
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
<i>18 variables</i>								
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

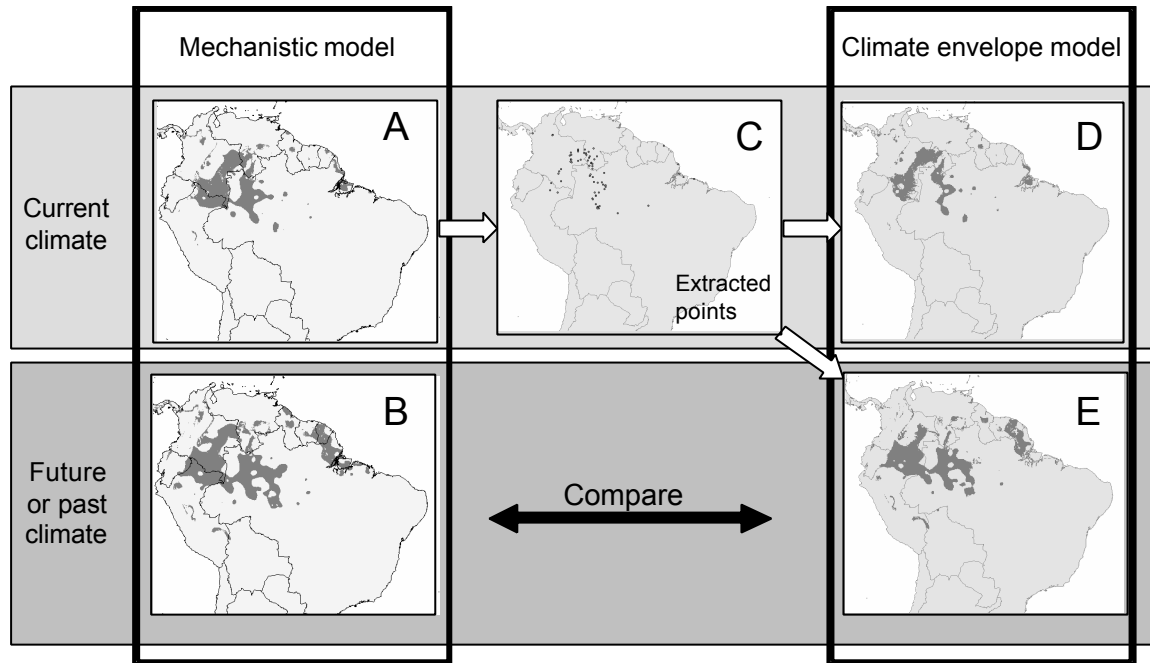


Fig 1. Approach used to evaluate the ability of climate envelope models to predict species distributions under different climates. A mechanistic model is used to predict the potential distribution for a species under current (A) and future (or past) (B) conditions (light gray = not suitable, dark gray = 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 are for *Berrya cordifolia* (Willd.) for the Bioclim model.

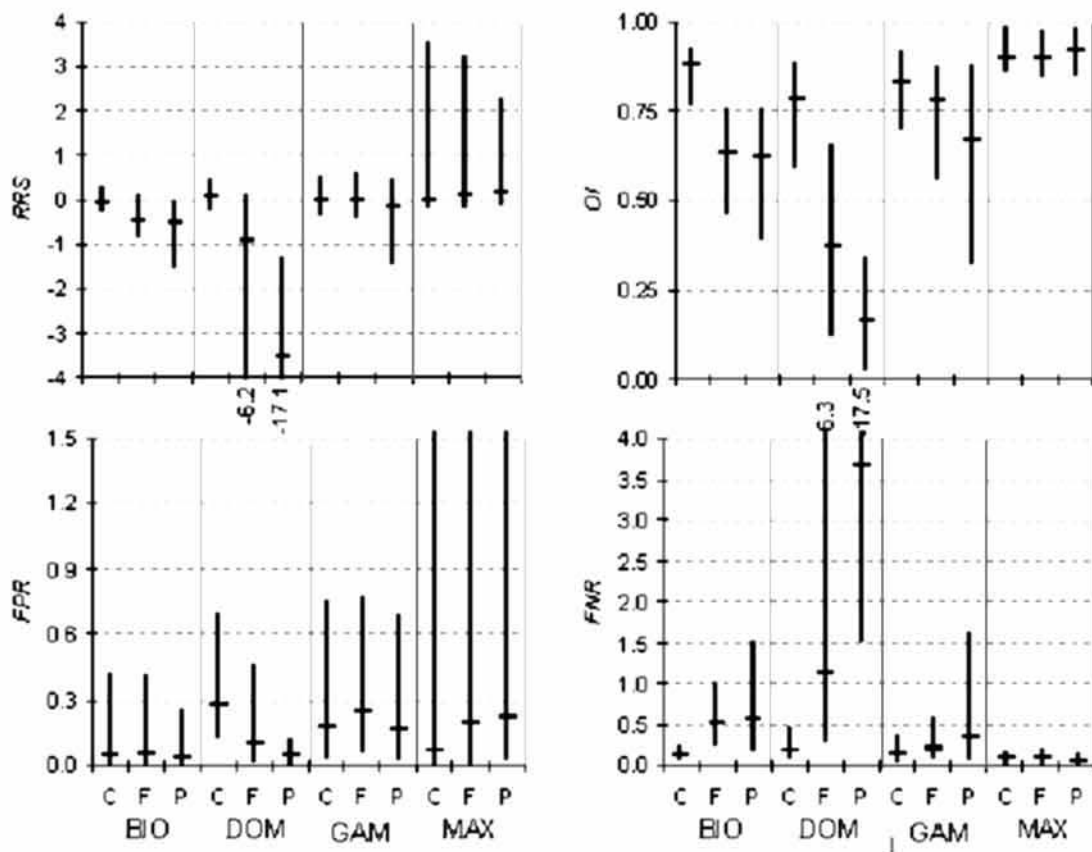
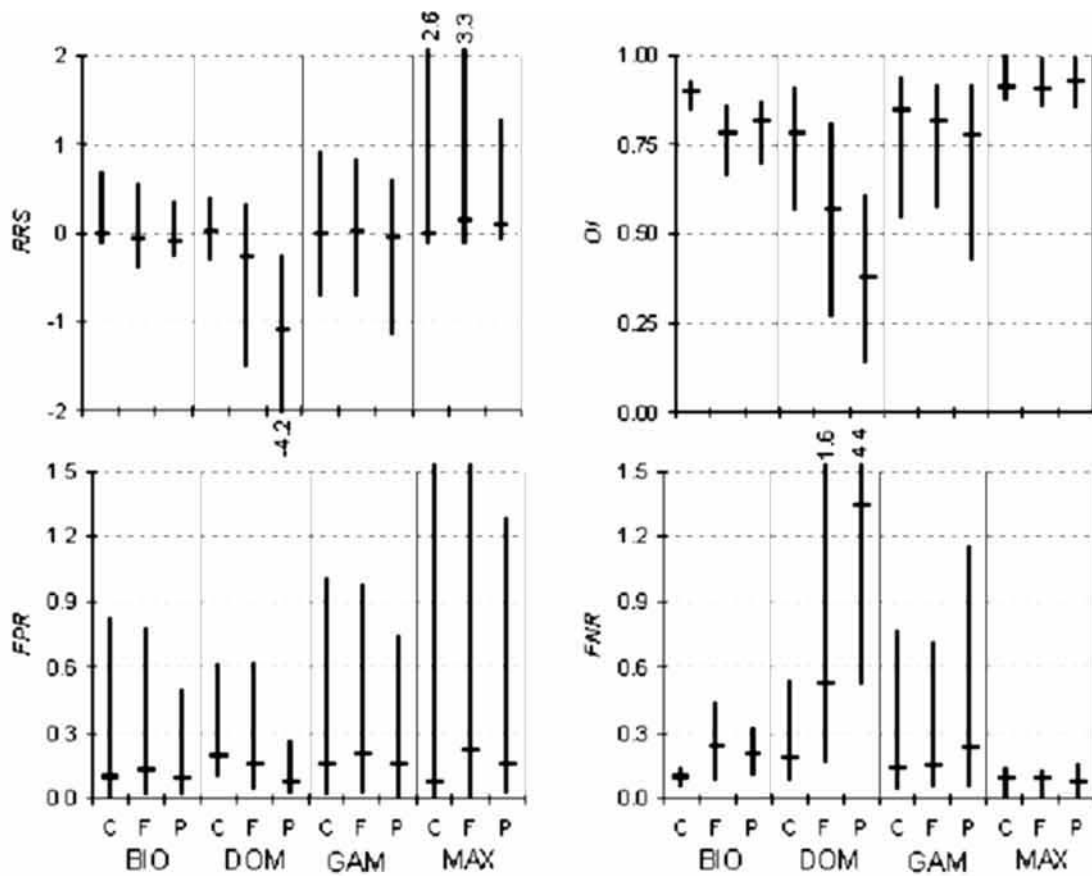
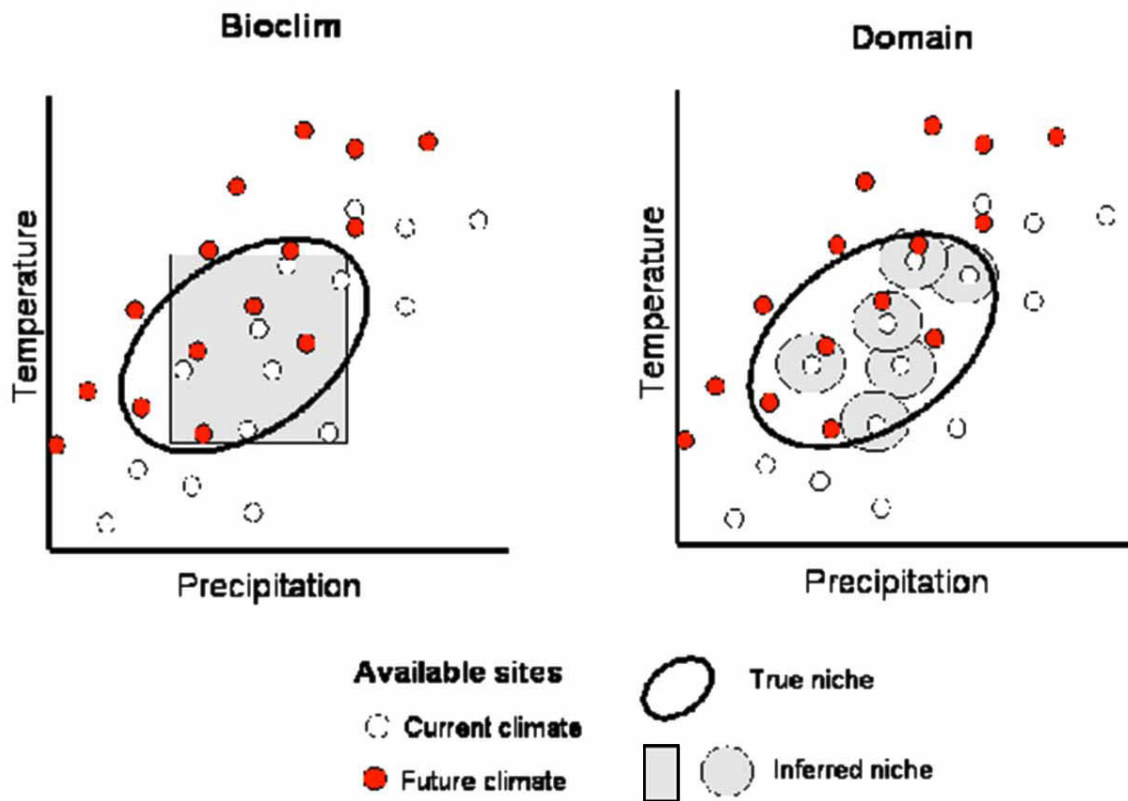


Fig. 2. Relative range size (*RRS*), overlap index (*OI*), false positive rate (*FPR*) and false negative rate (*FNR*) for a comparison between the results obtained with four climate envelope models, Bioclim (BIO), Domain (DOM), General Additive Modeling (GAM), and Maxent (MAX) and the results obtained 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×CO₂ 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.



2

3

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5 Fig. 3. Schematic description of predicting the distribution of a species under different

6 climates using two climate envelope models, Bioclim and Domain. There are 15 sites, with

7 different climates in the two time periods. The true requirements of the species are constant

8 and indicated with an ellipsoid. The inferred requirements do not fully overlap with the true

9 requirements because there are insufficient sites where the species has been observed and/or

10 because parts of the true niche are currently not present on the landscape, and because the

11 model methods are imperfect. Under future conditions, model performance is diminished

12 because some sites are incorrectly classified as not having the species (false negatives).