

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 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.

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 combina-

tion 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 CO₂ (2 × CO₂) 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° and longitude = -80°) 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 non-linear 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

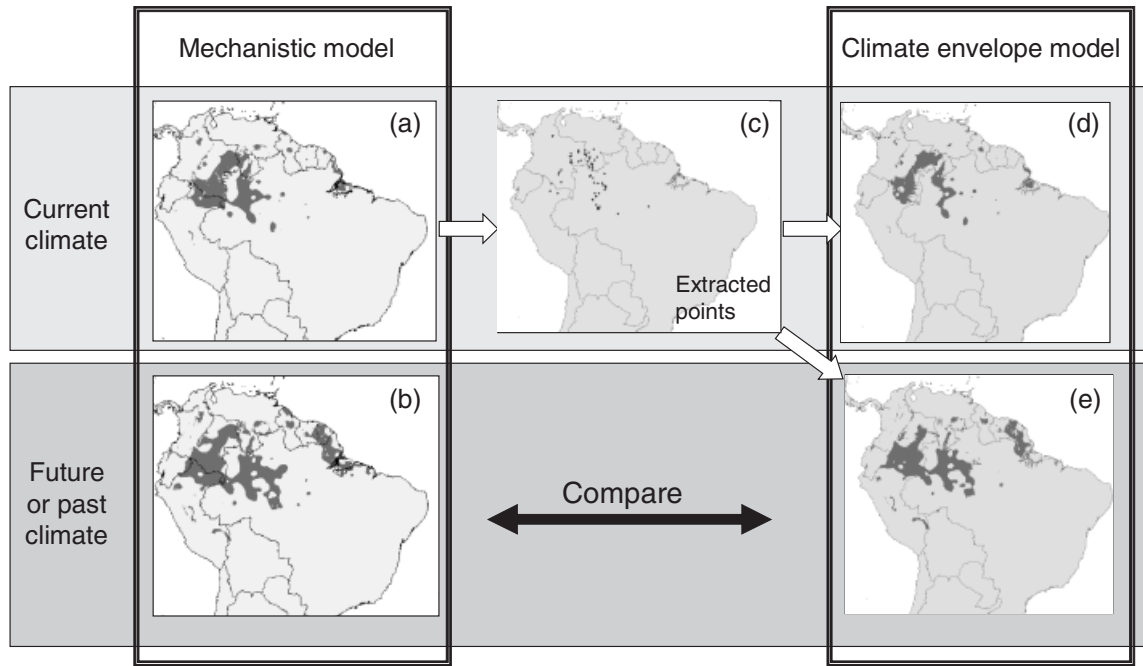


Fig. 1 Approach used to evaluate the ability of climate envelope models to predict species distributions under different climates. A mechanistic model is used to predict the potential distribution for a species under current (a) and future (or past) (b) conditions (light gray = not suitable, dark gray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

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

$$\text{OI} = o/m, \quad (2)$$

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

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

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

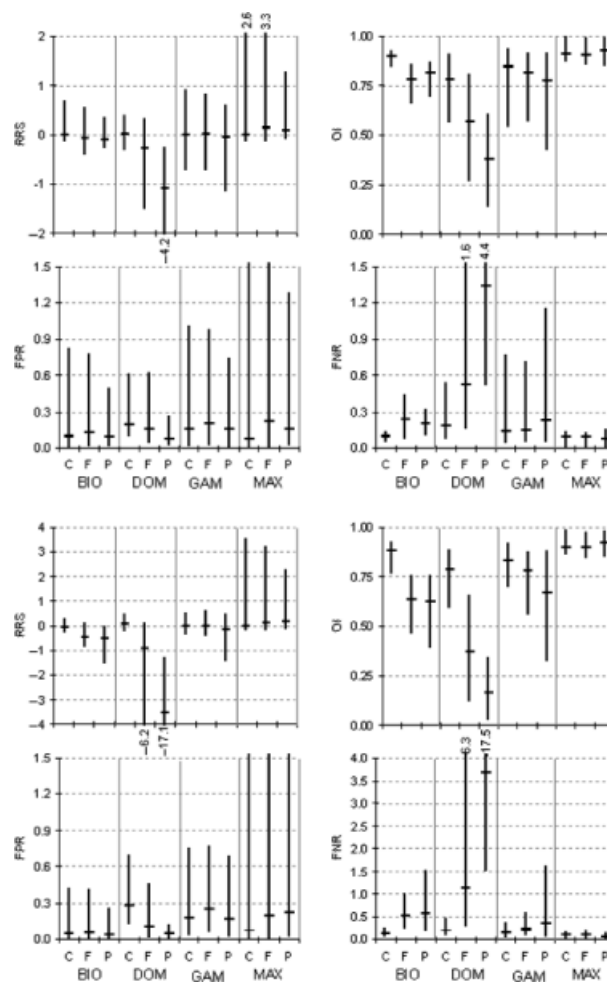


Fig. 2 Relative range size (RRS), overlap index (OI), false positive rate (FPR), and false negative rate (FNR) for a comparison between the results obtained with four climate envelope models, Bioclim (BIO), Domain (DOM), General Additive Modeling (GAM), and Maxent (MAX) and the results obtained with 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; $2 \times \text{CO}_2$ 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.

to those predicted with the MM (RRS ~ 0) and its OI was better than, or comparable with that of Bioclim.

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'

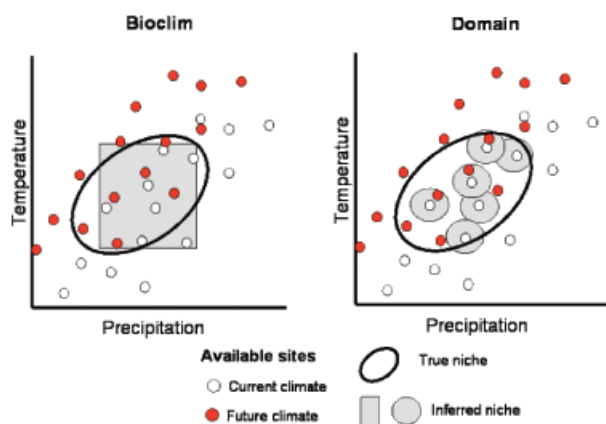


Fig. 3 Schematic description of predicting the distribution of a species under different climates using two climate envelope models, Bioclim, and Domain. There are 15 sites, with different climates in the two time periods. The true requirements of the species are constant and indicated with an ellipsoid. 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 dis-

tributions 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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References

- Araújo MB, Pearson RG (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.
- Araújo MB, Pearson RG, Thuiller W *et al.* (2005a) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Araújo MB, Whittaker RJ, Ladle RJ *et al.* (2005b) Reducing uncertainty in projects of extinction risk from climate change. *Global Ecology and Biogeography*, **14**, 529–538.
- 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 *et al.* (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 *et al.* (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Deutsches Klimarechenzentrum Modellbetreuungsgruppe (DKRZ) (1992) *The ECHAM3 atmospheric general circulation model*. DKRZ Technical Report 6. Deutsches Klimarechenzentrum, Hamburg.
- 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.
- Food and Agriculture Organization of the United Nations (FAO) (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 *et al.* (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and 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 USA*, **103**, 632–636.
- Guisan A, Thuiller W (2005) Predicting species distributions: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1003.
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hackett C (1991) *Plantgro: a software package for the coarse prediction of plant growth*. CSIRO, Melbourne.
- Hackett C, Vanclay JK (1998) Mobilizing expert knowledge of tree growth with the PLANTGRO and INFER systems. *Ecological Modelling*, **106**, 233–246.
- Hannah L, Midgley GF, Millar D (2002) Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, **11**, 485–495.
- Harte J, Ostling A, Green JL *et al.* (2004) Climate change and extinction risk. *Nature*, **430**, 36.
- Hijmans RJ (2003) The effect of climate change on global potato production. *American Journal of Potato Research*, **80**, 271–280.
- Hijmans RJ, Cameron SE, Parra JL *et al.* (2005a) Very high resolution interpolated global terrestrial climate surfaces. *International Journal of Climatology*, **25**, 1965–1978.
- Hijmans RJ, Garrett KA, Huamán Z *et al.* (2000) Assessing the geographic representative of genebank collections: the case of Bolivian wild potatoes. *Conservation Biology*, **14**, 1755–1765.
- Hijmans RJ, Guarino L, Bussink C *et al.* (2005b) *DIVA-GIS, version 5. Manual*. Available at <http://www.diva-gis.org/>
- Hugall A, Moritz C, Moussalli A *et al.* (2002) Reconciling paleodistribution models and comparative phylogeography in the wet tropics rainforest land snail *Gnarosiphia bellendenkerensis*. *Proceedings of the National Academy of Sciences USA*, **99**, 6112–6117.
- Hutchinson MF (1995) Interpolating mean rainfall using thin plate smoothing splines. *International Journal of Geographical Information Systems*, **9**, 385–403.

- Hutchinson MF (2004) *Anusplin version 4.3*. Centre for Resource and Environmental Studies. The Australian National University, Canberra.
- Kadmon R, Farber O, Danin A (2004) Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. *Ecological Applications*, **14**, 401–413.
- Kearney M, Porter WP (2004) Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, **85**, 3119–3131.
- La Sorte F (2006) Geographical expansion and increased prevalence of common species in avian assemblages: implications for large-scale patterns of species richness. *Journal of Biogeography*, **33**, 1183–1191.
- Lehmann A, Overton JMC, Leathwick JR (2002) GRASP: generalized regression analysis and spatial predictions. *Ecological Modelling*, **157**, 189–207.
- Lorenz S, Grieger B, Helbig P *et al.* (1996) Investigating the sensitivity of the atmospheric general circulation model EC-HAM 3 to paleoclimatic boundary conditions. *Geologische Rundschau*, **85**, 513–524.
- Malanson GP, Westman WE, Yan Y-L (1992) Realized versus fundamental niche functions in a model of chaparral response to climatic change. *Ecological Modelling*, **64**, 261–277.
- Martínez-Meyer E, Peterson AT, Hargrove WW (2004) Ecological niches as stable distributional constraints on mammal species, with implications for pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography*, **13**, 305–314.
- Midgley GF, Thuiller W (2005) Global environmental change and the uncertain fate of biodiversity. *New Phytologist*, **167**, 638–641.
- Miles L, Grainger A, Phillips O (2004) The impact of global climate change on tropical forest biodiversity in Amazonia. *Global Ecology and Biogeography*, **13**, 553–565.
- Nix HA (1986) A biogeographic analysis of Australian elapid snakes. In: *Atlas of Elapid Snakes of Australia*. *Australian Flora and Fauna Series No. 7* (ed. Longmore R), pp. 4–15. Australian Government Publishing Service, Canberra.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Pearson RG, Thuiller W, Araújo MB *et al.* (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704–1711.
- Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology*, **78**, 419–433.
- Peterson AT, Martínez-Meyer E, González-Salazar C (2004) Reconstructing the Pleistocene geography of the *Aphelocoma jays* (Corvidae). *Diversity and Distributions*, **10**, 237–246.
- Phillips SJ, Anderson R, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Prentice IC, Cramer W, Harrison SP *et al.* (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19**, 117–134.
- Randin CF, Dirnböck T, Dullinger S *et al.* (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689–1703.
- Root TL, Price JT, Hall KR *et al.* (2003) 'Fingerprints' of global warming on animals and plants. *Nature*, **421**, 57–60.
- Rosenzweig C, Parry ML (1994) Potential impact of climate change on world food supply. *Nature*, **367**, 133–138.
- Ruegg K, Hijmans RJ, Moritz C (2006) Climate change and the origin of migratory pathways in the Swainson's Thrush, *Catharus ustulatus*. *Journal of Biogeography*, **33**, 1172–1182.
- Theurillat J-P, Guisan A (2001) Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change*, **50**, 77–109.
- Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thuiller W (2003) BIOMOD—optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353–1362.
- Thuiller W (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology*, **10**, 2020–2027.
- Thuiller W, Araújo MB, Pearson RG *et al.* (2004) Biodiversity conservation – uncertainty in predictions of extinction risk. *Nature*, **430**, 36.
- Thuiller W, Richardson DM, Pyšek P *et al.* (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, **11**, 2234–2250.
- Van der Ploeg RR, Böhm W, Kirkham MB (1999) On the origin of the theory of mineral nutrition of plants and the law of the minimum. *Soil Science Society of America Journal*, **63**, 1055–1062.
- Wieczorek JR, Guo Q, Hijmans RJ (2004) The point-radius method for georeferencing point localities and calculating associated uncertainty. *International Journal of Geographic Information Science*, **18**, 745–767.
- Williams SE, Bolitho EE, Fox S (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London, Biological Sciences*, **270**, 1887–1892.
- Woodward FI, Rochefort I (1991) Sensitivity analysis of vegetation diversity to environmental change. *Global Ecology and Biogeography Letters*, **1**, 7–23.

18. A. Trumpp *et al.*, *Nature* **414**, 768 (2001).
19. M. N. Chamorro *et al.*, *EMBO J.* **24**, 73 (2005).
20. E. H. Jho *et al.*, *Mol. Cell. Biol.* **22**, 1172 (2002).
21. H. Lickert *et al.*, *Development* **132**, 2599 (2005).
22. M. Morkel *et al.*, *Development* **130**, 6283 (2003).
23. U. de Lichtenberg, L. J. Jensen, S. Brunak, P. Bork, *Science* **307**, 724 (2005).
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Materials and Methods

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Carbon-Negative Biofuels from Low-Input High-Diversity Grassland Biomass

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Biofuels derived from low-input high-diversity (LIHD) mixtures of native grassland perennials can provide more usable energy, greater greenhouse gas reductions, and less agrichemical pollution per hectare than can corn grain ethanol or soybean biodiesel. High-diversity grasslands had increasingly higher bioenergy yields that were 238% greater than monoculture yields after a decade. LIHD biofuels are carbon negative because net ecosystem carbon dioxide sequestration (4.4 megagram hectare⁻¹ year⁻¹ of carbon dioxide in soil and roots) exceeds fossil carbon dioxide release during biofuel production (0.32 megagram hectare⁻¹ year⁻¹). Moreover, LIHD biofuels can be produced on agriculturally degraded lands and thus need to neither displace food production nor cause loss of biodiversity via habitat destruction.

Globally escalating demands for both food (1) and energy (2) have raised concerns about the potential for food-based biofuels to be sustainable, abundant, and environmentally beneficial energy sources. Current biofuel production competes for fertile land with food production, increases pollution from fertilizers and pesticides, and threatens biodiversity when natural lands are converted to biofuel production. The two major classes of biomass for biofuel production recognized to date are monoculture crops grown on fertile soils (such as corn, soybeans, oilseed rape, switchgrass, sugarcane, willow, and hybrid poplar) (3–6) and waste biomass (such as straw, corn stover, and waste wood) (7–9). Here, we show the potential for a third major source of biofuel biomass, high-diversity mixtures of plants grown with low inputs on agriculturally degraded land, to address such concerns.

We performed an experiment on agriculturally degraded and abandoned nitrogen-poor sandy soil. We determined bioenergy production and ecosystem carbon sequestration in 152 plots, planted in 1994, containing various combinations of 1, 2, 4, 8, or 16 perennial herbaceous grassland species (table S1) (10). Species composition of each plot was determined by random draw from a pool of species. Plots were unfertilized, irrigated only during

establishment, and otherwise grown with low inputs (10). The 16-species plots are the highest diversity, or the LIHD (low-input, high-diversity), treatment. All plots were burned in early spring to remove aboveground biomass before growth began. Soil samples, collected before planting in 1994 and again in 2004, determined carbon sequestration in soil. Plots were sampled annually from 1996 to 2005 for aboveground biomass production.

Annual production of aboveground bioenergy (i.e., biomass yield multiplied by energy released upon combustion) (10) was an approximate log function of planted species number (Fig. 1A). On average for the last 3 years of the experiment (2003–2005), 2-, 4-, 8-, and 16-species plots produced 84%, 100%, 157%, and 238% more bioenergy, respectively, than did plots planted with single species. In a repeated measures multivariate analysis of variance, annual bioenergy production was positively dependent on the number of planted species ($F_{1, 155} = 68.4$, $P < 0.0001$), on time ($F_{9, 147} = 8.81$, $P < 0.0001$), and on a positive time-by-species number interaction ($F_{9, 147} = 11.3$, $P < 0.0001$). The interaction occurred because bioenergy production increased more through time in LIHD treatments than in monocultures and low-diversity treatments, as shown by the ratio of bioenergy in LIHD (16 species) plots to those in 8-, 4-, 2-, and 1-species plots (Fig. 1B).

The gross bioenergy yield from LIHD plots was 68.1 GJ ha⁻¹ year⁻¹. Fossil energy needed for biomass production, harvest, and transport to a biofuel production facility was estimated at 4.0 GJ ha⁻¹ year⁻¹ (table S2).

Different biofuel production methods capture different proportions of bioenergy in deliverable, usable forms (Fig. 2) (10). Cocombustion of degraded land LIHD biomass with coal in existing coal-fired electric generation facilities would provide a net gain of about 18.1 GJ ha⁻¹ as electricity (11). Converting LIHD biomass into cellulosic ethanol and electricity is estimated to net 17.8 GJ ha⁻¹ (12). Conversion into gasoline and diesel synfuels and electricity via integrated gasification and combined cycle technology with Fischer-Tropsch hydrocarbon synthesis (IGCC-FT) is estimated to net 28.4 GJ ha⁻¹ (10, 13). In contrast, net energy gains from corn and soybeans from fertile agricultural soils are 18.8 GJ ha⁻¹ for corn grain ethanol and 14.4 GJ ha⁻¹ for soybean biodiesel (14). Thus, LIHD biomass converted via IGCC-FT yields 51% more usable energy per hectare from degraded infertile land than does corn grain ethanol from fertile soils. This higher net energy gain results from (i) low-energy inputs in LIHD biomass production because the crop is perennial and is neither cultivated, treated with herbicides, nor irrigated once established and likely requires only phosphorus replacement fertilization because nitrogen is provided by legumes; (ii) the more than 200% higher bioenergy yield associated with high crop biodiversity; and (iii) the use of all aboveground biomass, rather than just seed, for energy. LIHD biofuels also provide much greater net energy outputs per unit of fossil fuel input than do current biofuels [net energy balance (NEB) ratios of Fig. 2]. Fertile lands yield about 50% more LIHD biomass (and bioenergy) than our degraded soils (15, 16).

Annual carbon storage in soil was a log function of plant species number (Fig. 1C). For 1994–2004, there was no significant net sequestration of atmospheric CO₂ in monoculture plots [mean net release of CO₂ of 0.48 ± 0.44 Mg ha⁻¹ year⁻¹ (mean ± SE)], but, in LIHD plots, there was significant soil sequestration of CO₂ (2.7 ± 0.29 Mg ha⁻¹ year⁻¹). Soil carbon storage occurred even though all aboveground biomass-based organic matter was removed annually via burning. Periodic resampling of soils in a series of prairie-like agriculturally degraded fields found C storage rates similar to those of the LIHD treatment and suggested that this rate could be maintained for a century (17). The observed annual rate of change in soil C at a particular soil depth declined with depth ($P = 0.035$), suggesting that an additional 5% more

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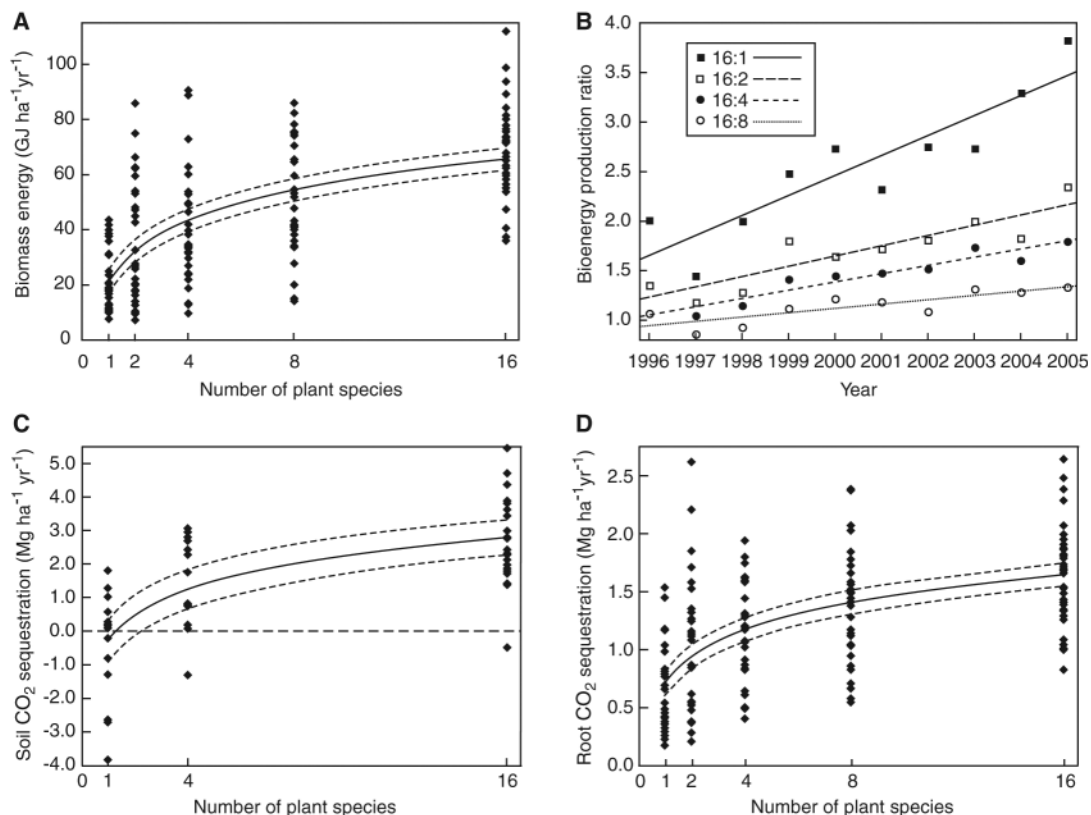


Fig. 1. Effects of plant diversity on biomass energy yield and CO₂ sequestration for low-input perennial grasslands. **(A)** Gross energy content of harvested aboveground biomass (2003–2005 plot averages) increases with plant species number. **(B)** Ratio of mean biomass energy production of 16-species (LIHD) treatment to means of each lower diversity treatment. Diverse plots became increasingly more productive over time. **(C)** Annual net increase in soil organic carbon (expressed as mass of CO₂ sequestered in upper 60 cm of soil) increases with plant diversity as does **(D)** annual net sequestration of atmospheric carbon (as mass of CO₂) in roots of perennial plant species. Solid curved lines are log fits; dashed curved lines give 95% confidence intervals for these fits.

C may be stored in soils deeper than we measured (below 60 cm depth).

In 2004, after 10 years of growth, atmospheric CO₂ sequestration in roots was a log function of plant species numbers (Fig. 1D). On an annual basis, 0.62 Mg ha⁻¹ year⁻¹ of atmospheric CO₂ was sequestered in roots of species grown in monocultures, and 160% more CO₂ (1.7 Mg ha⁻¹ year⁻¹) was captured in roots of 16-species plots. Multiple regression showed that root CO₂ sequestration (Mg ha⁻¹ of CO₂) increased as a log function of plant species number (*S*), as a log function of time (*Year*), and their interaction { $C_{\text{root}} = -1.47 + 6.16\log_{10}(S) + 9.64\log_{10}(\text{Year}) + 9.60[\log_{10}(S) - 0.613][\log_{10}(\text{Year}) - 0.782]$ where *Year* = 3 for 1997, the first time roots were sampled; overall $F_{3, 1260} = 191, P < 0.0001$; for $\log_{10}(S), F_{1, 1260} = 398, P < 0.0001$; for *Year*, $F_{1, 1260} = 148, P = 0.0001$; for $S \times \text{Year}, F_{1, 1260} = 27.3, P = 0.0001$ }. This regression suggests that most root carbon storage occurred in the first decade of growth; during the second decade, roots of 16-species plots are projected to store just 22% of C stored during the first decade. Measurements at greater depths in 10 LIHD plots suggest that 43% more C may be stored in roots between 30 and 100 cm.

LIHD plots had a total CO₂ sequestration rate of 4.4 Mg ha⁻¹ year⁻¹ in soil and roots during the decade of observation. Trends suggest that this rate might decline to about 3.3 Mg ha⁻¹ year⁻¹ during the second decade because of slower root mass accumulation. In

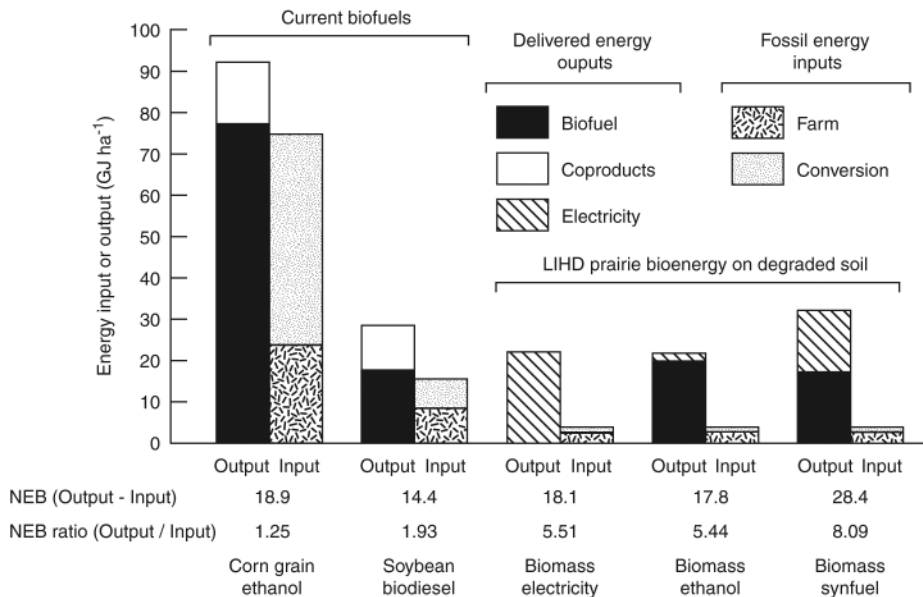


Fig. 2. NEB for two food-based biofuels (current biofuels) grown on fertile soils and for LIHD biofuels from agriculturally degraded soil. NEB is the sum of all energy outputs (including coproducts) minus the sum of fossil energy inputs. NEB ratio is the sum of energy outputs divided by the sum of fossil energy inputs. Estimates for corn grain ethanol and soybean biodiesel are from (14).

contrast, the annual rate of CO₂ sequestration for monocultures was 0.14 Mg ha⁻¹ year⁻¹ for the first decade and projected to be indistinguishable from zero for subsequent decades.

Across their full life cycles, biofuels can be carbon neutral [no net effect on atmospheric

CO₂ and other greenhouse gases (GHG)], carbon negative (net reduction in GHG), or carbon sources (net increase in GHG), depending on both how much CO₂ and other greenhouse gases, expressed as CO₂ equivalents, are removed from or released into the atmosphere

during crop growth and how much fossil CO₂ is released in biofuel production. Both corn ethanol and soybean biodiesel are net carbon sources but do have 12% and 41% lower net GHG emissions, respectively, than combustion of the gasoline and diesel they displace (14). In contrast, LIHD biofuels are carbon negative, leading to net sequestration of atmospheric CO₂ across the full life cycle of biofuel production and combustion (table S3). LIHD biomass removed and sequestered more atmospheric CO₂ than was released from fossil fuel combustion during agriculture, transportation, and processing (0.32 Mg ha⁻¹ year⁻¹ of CO₂), with net life cycle sequestration of 4.1 Mg ha⁻¹ year⁻¹ of CO₂ for the first decade and an estimated 2.7 to 3 Mg ha⁻¹ year⁻¹ for subsequent decades. GHG reductions from use of LIHD biofuels in lieu of gasoline and diesel fuel are from 6 to 16 times greater than those from use of corn grain ethanol and soybean biodiesel in lieu of fossil fuels (Fig. 3A).

LIHD biofuel production should be sustainable with low inputs of agrichemicals, as in our study. Legumes in LIHD plots can supply nitrogen (18). In our experiment, total soil nitrogen of LIHD plots increased 24.5% ($P < 0.001$) from 1994–2004, but monoculture total soil nitrogen was unchanged ($P = 0.83$). However, some amount of N fertilization may be useful in dry habitats that lack efficient N-fixing species. Application of P or other nutrients may be needed if initially limiting or to replace nutrient exports (Fig. 3B). Production may be sustainable with low pesticide use, because plant disease incidence and invasion by exotic species are low in high-diversity plant mixtures (Fig. 3C) (19).

Switchgrass (*Panicum virgatum*), which is being developed as a perennial bioenergy crop,

was included in our experiment. Switchgrass monocultures can be highly productive on fertile soils, especially with application of pesticides and fertilizer (20, 21). However, on our infertile soils, switchgrass monoculture bioenergy [23.0 ± 2.4 GJ ha⁻¹ year⁻¹ (mean ± SE)] was indistinguishable from mean bioenergy of monocultures of all other species (22.7 ± 2.7 GJ ha⁻¹ year⁻¹) and yielded just a third of the energy of LIHD plots (10).

How much energy might LIHD biomass potentially provide? For a rough global estimate, consider that about 5 × 10⁸ ha of agriculturally abandoned and degraded land producing biomass at 90 GJ ha⁻¹ year⁻¹ (22) could provide, via IGCC-FT, about 13% of global petroleum consumption for transportation and 19% of global electricity consumption (2). Without accounting for ecosystem CO₂ sequestration, this could eliminate 15% of current global CO₂ emissions, providing one of seven CO₂ reduction “wedges” needed to stabilize global CO₂ (23). GHG benefits would be larger if LIHD biofuels were, in general, carbon negative, as might be expected if late-successional native plant species were used in LIHD biomass production on degraded soils [e.g., (17)].

The doubling of global demand for food and energy predicted for the coming 50 years (1, 2) and the accelerating use of food crops for biofuels have raised concerns about biodiversity loss if extant native ecosystems are converted to meet demand for both food and biofuels. There are also concerns about environmental impacts of agrichemical pollution from biofuel production and about climate change from fossil fuel combustion (14, 24–26). Because LIHD biomass can be produced on abandoned agricultural lands, LIHD biofuels

need neither compete for fertile soils with food production nor encourage ecosystem destruction. LIHD biomass can produce carbon-negative biofuels and can reduce agrichemical use compared with food-based biofuels. Moreover, LIHD ecosystem management may provide other ecosystem services, including stable production of energy, renewal of soil fertility, cleaner ground and surface waters, wildlife habitat, and recreation (18, 19, 24, 27, 28). We suggest that the potential for biofuel production and carbon sequestration via low inputs and high plant diversity be explored more widely.

References and Notes

- N. Fedoroff, J. Cohen, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 5903 (1999).
- International Energy Outlook* (DOE/EIA-0484, Energy Information Administration, U.S. Department of Energy, Washington, DC, 2006).
- A. E. Farrell *et al.*, *Science* **311**, 506 (2006).
- J. Outlaw, K. Collins, J. Duffield, Eds., *Agriculture as a Producer and Consumer of Energy* (CABI, Wallingford, UK, 2005).
- G. Keoleian, T. Volk, *Crit. Rev. Plant Sci.* **24**, 385 (2005).
- I. Lewandowski, J. Scurlock, E. Lindvall, M. Christou, *Biomass Bioenergy* **25**, 335 (2003).
- P. Gallagher *et al.*, *Environ. Resour. Econ.* **24**, 335 (2003).
- Y. Zhang, M. Dubé, D. McLean, M. Kates, *Bioresource Technol.* **89**, 1 (2003).
- S. Kim, B. Dale, *Biomass Bioenergy* **26**, 361 (2004).
- Materials and methods are available as supporting material on Science Online.
- M. Mann, P. Spath, *Clean Prod. Process.* **3**, 81 (2001).
- J. Sheehan *et al.*, *J. Ind. Ecol.* **7**, 117 (2003).
- C. Hamelinck, A. Faaij, H. den Uil, H. Boerrigter, *Energy* **29**, 1743 (2004).
- J. Hill, E. Nelson, D. Tilman, S. Polasky, D. Tiffany, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 11206 (2006).
- P. Camill *et al.*, *Ecol. Appl.* **14**, 1680 (2004).
- C. Owensby, J. Ham, A. Knapp, L. Auen, *Global Change Biol.* **5**, 497 (1999).
- J. Knops, D. Tilman, *Ecology* **81**, 88 (2000).
- D. Tilman *et al.*, *Science* **294**, 843 (2001).
- J. Knops *et al.*, *Ecol. Lett.* **2**, 286 (1999).
- D. Parrish, J. Fike, *Crit. Rev. Plant Sci.* **24**, 423 (2005).
- K. Vogel, J. Brejda, D. Walters, D. Buxton, *Agron. J.* **94**, 413 (2002).
- M. Hoogwijk *et al.*, *Biomass Bioenergy* **25**, 119 (2003).
- S. Pacala, R. Socolow, *Science* **305**, 968 (2004).
- P. M. Vitousek, H. A. Mooney, J. Lubchenco, J. M. Melillo, *Science* **277**, 494 (1997).
- D. Tilman *et al.*, *Science* **292**, 281 (2001).
- G. Berndes, *Global Environ. Change* **12**, 253 (2002).
- J. A. Foley *et al.*, *Science* **309**, 570 (2005).
- D. Hooper *et al.*, *Ecol. Monogr.* **75**, 3 (2005).
- Agricultural Chemical Usage 2004 and 2005 Field Crops Summaries* (National Agricultural Statistics Service, U.S. Department of Agriculture, Washington, DC, 2006).
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Supporting Online Material

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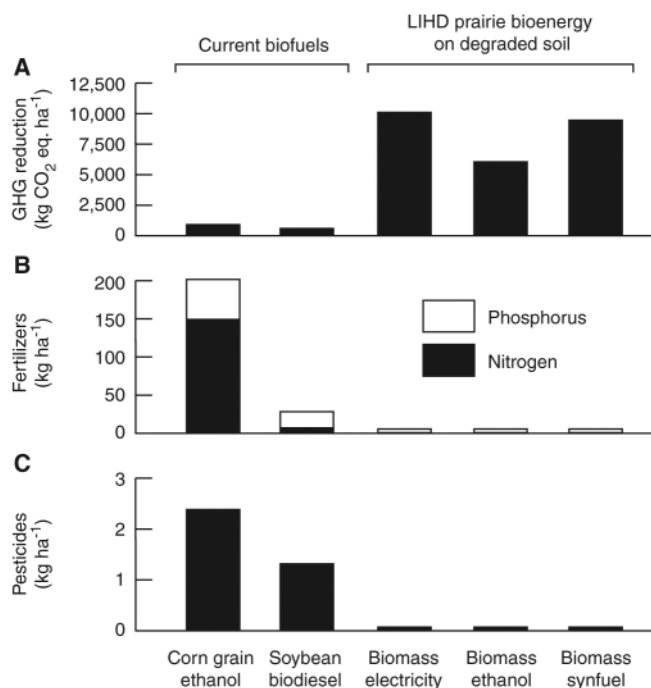
Materials and Methods

Tables S1 to S3

References

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Fig. 3. Environmental effects of bioenergy sources. **(A)** GHG reduction for complete life cycles from biofuel production through combustion, representing reduction relative to emissions from combustion of fossil fuels for which a biofuel substitutes. **(B)** Fertilizer and **(C)** pesticide application rates are U.S. averages for corn and soybeans (29). For LIHD biomass, application rates are based on analyses of table S2 (10).



What Is Natural? The Need for a Long-Term Perspective in Biodiversity Conservation

K. J. Willis^{1*} and H. J. B. Birks²

Ecosystems change in response to factors such as climate variability, invasions, and wildfires. Most records used to assess such change are based on short-term ecological data or satellite imagery spanning only a few decades. In many instances it is impossible to disentangle natural variability from other, potentially significant trends in these records, partly because of their short time scale. We summarize recent studies that show how paleoecological records can be used to provide a longer temporal perspective to address specific conservation issues relating to biological invasions, wildfires, climate change, and determination of natural variability. The use of such records can reduce much of the uncertainty surrounding the question of what is “natural” and thereby start to provide important guidance for long-term management and conservation.

Paleoecological records (e.g., fossil pollen, seeds and fruits, animal remains, tree rings, charcoal) spanning tens to millions of years provide a valuable long-term perspective on the dynamics of contemporary ecological systems (1). Such studies are increasingly becoming part of community and landscape ecological research (2). In contrast, conservation-related research largely ignores paleoecological records. For example, there are no temporal records spanning more than 50 years included in any of the key biodiversity assessments published over the past 7 years (3). Paleoecological records have been considered too descriptive and imprecise, and therefore of little relevance to the actual processes of conservation and management. Such criticisms may have been valid 30 years ago, but there is now a wealth of information in paleoecological records providing detailed spatial and temporal resolutions (1, 4–7) that match in detail most records currently used in conservation research.

The potential of paleoecological records in conservation biology has been highlighted several times, including their application to biodiversity maintenance, ecosystem naturalness, conservation evaluation, habitat alteration, changing disturbance regimes, and invasions [e.g., (8–14)]. Conservation of biodiversity in a changing climate (15) and the relevant temporal and spatial scales for ecological restoration (16) have also been considered to warrant a longer-term temporal perspective. Most of

these studies are descriptive and provide little practical application. A number of recent applied paleoecological studies, however, have begun to provide direct management information for biodiversity conservation at local, regional, and global scales. These include recommendations relating to biological invasions, wildfires, climate change, and conservation management within thresholds of natural variability. The overriding message from these studies is that such temporal perspectives are essential for meaningful modeling, prediction, and development of conservation strategies in our rapidly changing Earth.

Biological Invasions

Biological invasions are of critical concern to conservation organizations worldwide, with a general perception that many invasives are responsible for widespread community change and even extinctions (17). At the Rio Earth Summit Convention on Biological Diversity in 1992, for example, binding signatories were made “to prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species” (18). However, biological invasions are complex. Some regions are more prone to invasion, certain species are more successful invaders than others, and sometimes it is even unclear whether a species is alien or native. The importance of the historical record in improving our ability to predict the outcome of

non-native introductions has been acknowledged [e.g., (13, 14)], but several recent paleoecological studies provide direct guidelines for the identification and management of invasives.

The distinction between what is native and what is not is often unclear. A species is usually classified as either native or exotic according to whether it is located in its presumed area of evolutionary origin and/or whether human agency is responsible for its current distribution. In the absence of a temporal record to assess a species history, the distinction can often become blurred (16). For example, in a reexamination of the British flora, several discrepancies between published records were found, with the same species being classified as “alien” or “native” depending on personal interpretation (19) (Table 1). There is also the question of how far back one takes “human” activity in determining whether a species is native or alien. When using evidence of first occurrences of species based on paleoecological records to reassess “doubtful natives” in the British flora, Preston *et al.* (19) determined that at least 157 plant species had been introduced to Britain by humans, intentionally or unintentionally, from the start of the Neolithic period (about 4000 years ago) to 500 years ago, yet the terminology used for their classification according to different floras is highly variable (Table 1). Preston *et al.* proposed that such species should be classified separately as “archaeophytes.” They acknowledged, however, that this causes problems with their conservation status because this “non-native” label excludes them from the British Red Data Book of threatened or near-extinct species, and automatically deems them to be of lower conservation value—even though some are in serious decline and have been part of the British flora for at least 500 years.

A similarly conflicting conservation message was reached in an applied paleoecological study on the origin of an invasive form of the common reed (*Phragmites australis*) in the marshes of the inland wetlands of Lake Superior, North America (20) (Fig. 1). Over recent decades, *P. australis* populations have expanded rapidly throughout the coastal wetlands of North America, creating substantial changes in community structure and composition. In this study, paleoecological and genetic analyses were used to determine when the common reed became established in this region and whether the source was from a native or non-native

Table 1. Classification of 157 species of British plants that were probably introduced more than 500 years ago (archaeophytes) according to three published floras (54–56).

Published flora	Native	Doubtful native	Introduced	Probably introduced	Uncertain or untreated	Total
Dunn, 1905 (54)	31	—	103	—	23	157
Clapham <i>et al.</i> , 1952 (55)	85	19	30	10	13	157
Stace, 1991 (56)	77	27	39	14	0	157

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population. A 4000-year paleoecological record indicated that reeds were not part of the local flora until very recently (several decades), and that their recent expansion was probably linked to changes in water levels in the wetlands and human-induced changes to the landscape. The simple conservation message from this study is therefore to eradicate or control reed populations, because the expansion was recent and is likely to cause serious changes to the wetlands community. However, genetic data from these reed populations add another level of complexity because they indicate that the reeds are a native variety, raising the question of whether this is an exotic or natural invasion.



Fig. 1. Native (?) common reed (*Phragmites australis*) growing in Bark Bay Slough on Lake Superior, North America [photo: E. A. Lynch]; rattlesnake (*Crotalus mitchellii stephensi*) in the warm desert of western North America [photo: Blake L. Thompson]; wood grouse or western capercaillie (*Tetrao urogallus*) in the Cantabrian Mountains, northern Spain [photo: E. Menoni].

Oceanic islands are particularly liable to invasions, and it is often difficult to assess whether particular species are native or introduced. The invasive ornamental club moss *Selaginella kraussiana*, for example, is widely planted in the Neotropics, southern United States, Australasia, and western Europe. It is common on the Azores Islands in a range of habitats, but is it native there? Paleoecological records (21) (Fig. 2) clearly show that *S. kraussiana* had been present on Flores in the Azores for several thousand years before Portuguese discovery and Flemish settlement in the 15th century, thereby establishing beyond doubt its native status on Flores Island. Paleoecology again helped here to resolve a question in biodiversity conservation.

Another key question is whether invasive species are the triggering mechanism for ecosystem change, or merely opportunists taking advantage of environmental change caused by other biotic or abiotic factors? Also, are there particular factors that make a habitat more susceptible to invasion? A study of the colonization and spread of invasive shrubs in native shrublands and early successional forests in the northeastern United States, for example, found that prevalence of agricultural fields (historic and present-day) was the most influential factor affecting the colonization and spread of invasive shrubs (22). These native shrublands and early successional forests currently have high conservation status because of their diversity of terrestrial vertebrates. By considering the temporal dimension, the authors argue that it should be possible to identify those early successional habitats that may be especially prone to exotic invasion and ought to be of higher conservation

priority. This study used only 40 years of temporal data, but studies incorporating longer temporal time scales have also illustrated persistent legacies of ancient land use that may influence the vulnerability of a site to invasion (12), including differences in soil pH, C, and N values. These imprints can last for decades to centuries. The identification of former land use by paleoecological records can thus be a tool for understanding and determining a habitat's vulnerability to invasion.

Introductions of non-native species often appear to fail a number of times before they eventually succeed; therefore, there is a lag between first colonization and population expansion of the invasive species (23). The reasons for resistance to invasion are complex and can have as much to do with environmental variables and extreme events as with demographic and biotic factors (6, 7). A study using paleoecological records has shown that consideration should be given to biological inertia (24), whereby a native community occurs where environmental conditions are no longer optimal but will remain in situ without any triggering mechanism (e.g., hurricanes, windthrow, etc.) to "remove" this resident population. Thus, the life history characteristics and biology of the resident species, and not the properties of the invading species, are responsible for invasion lags. This phenomenon is particularly apparent in forest ecosystems. In many current old-growth forests in western North America, paleoecological studies have shown that these stands were established during the cooler and moister climate of the Little Ice Age (about 650 to 150 years ago) and therefore reflect recruitment responses to former climate conditions (25). Such information about ecological legacies (1) is directly relevant to conservation because such forests may be at a critical threshold and may be particularly vulnerable to invasion after a disturbance event, either natural or human-induced.

Wildfires

Wildfires have been important in shaping the structure and function of fire-prone communities throughout Earth's history (26). Of particular concern to conservationists, however, are changes in the frequency, severity, and extent of burning from those perceived as the "norm" (27). What processes are driving this change (human or climate)? How will it affect the composition of plants and animals in ecosystems, in particular those already identified as vulnerable? And are there particular management techniques

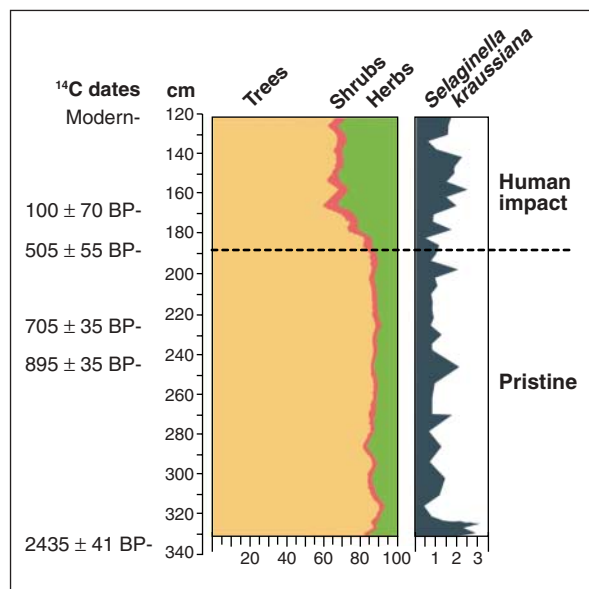


Fig. 2. Simplified pollen diagram for Lagoa Rasa, Flores Island, Azores, for the past 3000 years showing the percentage of tree, shrub, and herb pollen and of *Selaginella kraussiana* spores before and after human occupation of the island. [Modified from (21)]

that can be implemented to alter fire regimes? Fundamental to these questions is establishing the natural variability of wildfires so that this can be used as a benchmark against which to evaluate contemporary conditions and future alternatives (28). Assessments based on short-term records (<50 years) can easily lead to misguided management plans (29).

Although climate change and human activities have long been acknowledged as drivers of wildfires, results from recent paleoecological studies show that these relationships are complex. For example, although it is not unreasonable to assume that an increase in aridity would result in more fires, several studies indicate otherwise. In the Alaskan boreal forest, fires occurred more frequently under wetter climatic conditions (30). A similar conclusion was reached in a paleoecological study of fire cycles in the Northern Great Plains grasslands of North America (31). Here, the highest charcoal flux occurred during past moist intervals when grass cover was extensive and fuel loads were high. Shifts in fuel quantity and quality can cause changes in fire regimes. Both studies show that there is a complex climate-fuel-fire relationship determining the variability of wildfires (32). Such studies (33) should be taken into account when predicting future ecosystem change within climate change conservation strategies.

Prehistoric and historic human-induced wildfires are often assumed to have caused changes in ecosystem structure and degradation, especially in tropical forests where natural fires are rare and tend to be limited in extent. Management plans to control such fires are usually implemented, however, without paleoecological evidence to confirm such an assumption. One such example is in the tropical dry forests of the southern Ratanakiri Province, northeastern Cambodia (34). Here, regional conservation policy is based on the premise that burning by humans has degraded the dense forests and resulted in the present open forest-savanna mosaic. However, a paleoecological study shows that present-day fire activity is now lower than it has been for the past 9300 years (Fig. 3). Rather, the forest-savanna shift is probably a consequence of monsoonal activity, and the high-frequency but low-intensity fires caused by humans may, in fact, conserve forest cover. In this case, the current conservation management plan is clearly at odds with evidence from the paleoecological record.

Interesting conclusions have also emerged from studies examining ecosystem composition in response to fire regimes. One of the main

findings of the work on the North American grasslands described above, for example, is that fire is not necessarily a universal feature of this ecosystem but oscillates through time with climate (31). The impact of such variability in burning regimes through time on ecosystem composition can have conservation implications. This is well illustrated in a study on the long-term record of fire and open canopy in a forest in southern Sweden that contains an exceptionally large number of endangered species of beetle (35). Of the 105 beetle species recorded at this site living on or in rotting wood that are in the Swedish Red Data Book of threatened or near-extinct species, many are associated with open forest, forest fires, or structures created by fire. Yet a site-scale paleoecological study indicates that the forest is more closed today than at any time in the past 2500 years; although

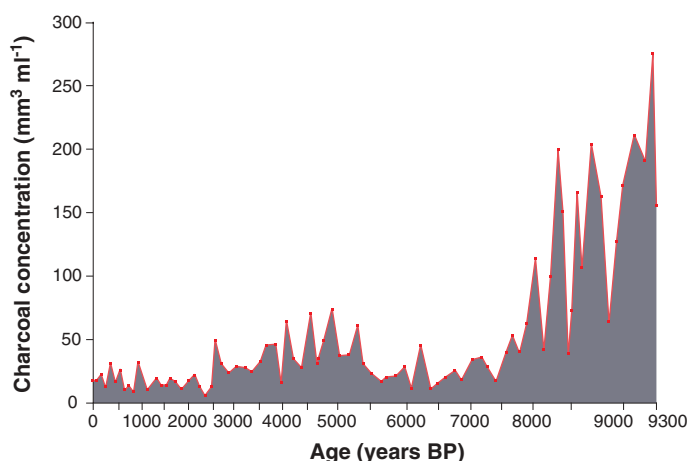


Fig. 3. Reconstructed fire regimes in northeastern Cambodian monsoonal forests over the past 9300 years, using microfossil charcoal concentration from a dated sedimentary sequence (34). The record indicates that present-day charcoal input is the lowest of the entire period. Conservation policies that suggest that human burning has increased and resulted in the open forest-savanna mosaic in this region are clearly misguided, as are management recommendations for fire suppression.

there had been a significant amount of burning in the past, there has been a large reduction in fires over the past 200 years. The authors concluded that openness of the site in the past as a consequence of burning is an important explanation for the high conservation value of the site today (35). To conserve the diverse beetle assemblage of this site, they suggested that open forest conditions needed to be restored and that prescribed burns would be the most appropriate way to achieve this.

Climate Variability

Most conservation organizations have developed climate change conservation strategies [as described in (36)] designed to conserve biodiversity in a changing climate. Two questions central to current conservation strategies arise. Where will biota move to in response to future climate change? Which species and regions are

most at risk from future climate change? Underlying these questions are key management and planning issues—for example, ensuring that reserve boundaries allow for potential species-range shifts (37) and that the species and regions most at risk are identified and protected (38).

In the evaluation of predictive models to determine the biogeographic effects of climate change, several studies have used paleoecological records for backward prediction (hindcasting) to assess errors potentially inherent in species-envelope bioclimatic modeling (39). This involves running models for past intervals of time, using present-day species data but modeling the species' response to climate change against paleoclimatic data as opposed to present-day climatic data. The predicted distributions are then tested against the distribution of the species apparent in the fossil record for the time interval

covered by the paleoclimatic data to assess model robustness (40). In a study of 23 extant mammal species in the United States (39), for example, an ecological niche model was run backward for the time interval of the Last Full Glacial (14,500 to 20,500 years before the present) and predicted distributions were compared to actual distribution records obtained from the FAUNMAP fossil database (41). The model was also run in reverse (i.e., using fossil data and paleoclimatic data to predict present distributions) and similar comparisons were made. Results indicated that for nine species the model was able to predict accurately the Pleistocene distributions from the present-day data, and vice versa. Not only did this confirm that the model was robust for these species, it also provided a test for the underlying assumption of these models that the species' ecological

niche characteristics have remained constant through time. A similar pattern was recently found for several North American plant species (42). The remaining species, however, either had significant predictions only one way but not the other (nine species) or were not significant in either direction (five species).

The question of why some species' distributions cannot be accurately predicted by species-climate modeling can also be answered, at least for some species, from paleoecological studies. A study of the spread of *Picea abies* (spruce) and *Fagus sylvatica* (beech) over the past 4000 years in southern Scandinavia, for example, showed that at the local-stand scale the spread of *Picea* closely tracked the changing area of suitable regional climate, whereas the spread of *Fagus* was more directly linked to anthropogenic activities and disturbance by fire (43). Thus, caution may be needed in using the results of

predictive species-envelope models in conservation planning, because the distributions of some species today or in the past may be poorly predicted.

Bioclimatic models are particularly relevant to conservationists in determining and understanding the dynamics of the leading edge of species-range margins and the potential space that will be needed for future reserve boundaries (40). There is also a considerable literature on modeling to determine which species will go extinct [e.g., (38)]. However, there are few studies of the likely fate of rear-edge populations, that is, the source populations from which the leading-edge populations migrate (Fig. 4) (44). A key conservation objective should be the preservation of conditions necessary for speciation (45). Evidence from paleoecological and genetic records indicates that the maintenance of populations in these rear-edge regions could, in fact, be critical for conservation of long-term genetic diversity (44). Evidence also suggests that these regions tend to be where plants and animals were geographically and genetically isolated in refugia during the cold stages of the Pleistocene. In Europe, for example, refugial localities have been recognized in Iberia, the Balkans, and Italy and in mountain ranges such as the Carpathians (46–48).

With the use of a combination of paleoecological and genetic evidence, other such regions have been identified, and this information is feeding into conservation policy. For example, in a study on Eurasian populations of western capercaillie (grouse)—a keystone species of Palearctic boreal and high-altitude coniferous forests (49)—a combined genetic and temporal record enabled the identification of two regions that should be classified as ecologically significant units (ESUs) because of the genetic distinctiveness of the populations within them from the rest of Europe. The distinctiveness of the populations in these ESUs, located in the Pyrenees and Cantabrian Mountains (Fig. 1), is almost certainly related to their Pleistocene refugial isolation. Similar historically related genetic patterns have been identified in these two regions for a number of plants and animals, and this knowledge is now leading to international recognition of the conservation importance of these areas (49).

In the United States, a similar approach using a molecular and deep-time historical perspective as a primary mechanism to frame biodiversity reserves (50) has been applied to a number of groups of plants and animals. Distinctive patterns of genetic diversity related to geological events in deep time (Pliocene/Miocene) and to Pleistocene refugial isolation have been demonstrated, for example, in four rattlesnake species (Fig. 1; genus *Crotalus*) in the warm deserts of western North America (50). Here it is argued that an approach that seeks to understand the causation of genetic patterns would be more effective in encapsulating biodiversity than

current measures (based on the use of geological features as a surrogate for diversity) and that such studies should be routinely used in developing integrated regional conservation policies (50).

Determination of Thresholds Within Natural Variability

Variability through time is an inherent part of ecosystem behavior. It is thus essential to incorporate variability into management policies. To do this reliably in our rapidly changing world requires answers to several questions. What are the baseline or “reference” conditions before recent times? What is the range of natural variability? Under what conditions do negative impacts become apparent? How can thresholds be determined beyond which specific management plans should be implemented?

Gillson and Duffin (51) used paleoecological records from savannas in Kruger National Park, South Africa, to determine the natural variability of woody vegetation cover during the past 5000 years. They used this information to address whether woody cover has decreased below 80% of its “highest ever value”—a threshold set by ecosystem managers to define the upper and lower level of accepted variation in this ecosystem. Paleoecological results indicated that during the past 5000 years, the estimated woody vegetation cover had remained at about 20% of its “highest ever value,” and therefore that management intervention in this part of the park is unnecessary at present.

Other examples where paleoecological records have been used to identify where natural thresholds have recently been exceeded include river ecosystems in Australia (52) and Colorado (53). The large deep billabongs in the middle reaches of the Murray River, Australia, for example, do not currently support submerged mac-

rophyte beds. Yet paleoecological analyses indicate that these were an important part of the ecosystem before the arrival of Europeans (52). In the Colorado delta ecosystem (53), paleoecological studies suggest that there has been a decline of up to 94% of shelly benthic macroinvertebrates over the past 75 years. This decline is probably associated with a reduction of fresh water and nutrients resulting from the diversion of the Colorado River by dams and irrigation projects. Both studies provide quantitative assessments of the relative health (4) of these river ecosystems and indicate thresholds that have been exceeded—information that is critical to their restoration and long-term conservation.

Conclusions

Conservation biology and nature management are primarily concerned with the present and increasingly with the future. Paleoecology primarily considers the past but can provide a historical perspective to the present (1). It can also contribute to key questions in conservation and management such as habitat naturalness, biological invasions, disturbance regimes, natural variability, and ecosystem health. With increasing amounts of paleoecological data of a high spatial and/or temporal resolution (4, 5), there is potential for synergy between conservation biology and paleoecology. There are, however, several research needs and challenges that need to be met before an effective synergy can fully develop. These include the following:

- 1) Paleoecological studies in biodiversity hotspots with a high density of species. At present there are few studies from these critical areas.
- 2) Improved taxonomic resolution of the fossils found, because improved resolution invariably enhances the biological value of fossil records (5, 21).

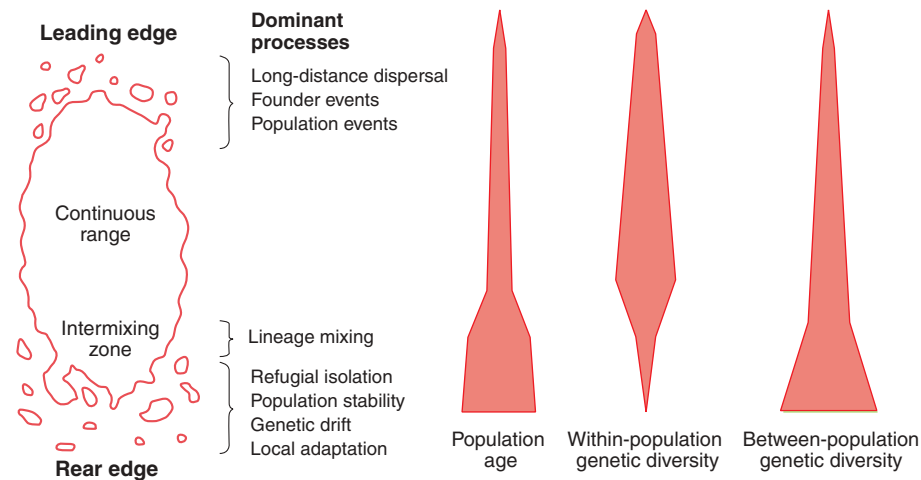


Fig. 4. Schematic representation of the leading and rear-edge populations in response to climate change (44). Paleoecological and genetic evidence suggests that the rear-edge populations may be extremely important in the conservation of long-term genetic diversity and that more attention must be given to modeling the impacts of future climate change on these populations and their protection.

3) Assessing terrestrial paleoecological data in terms of “ecosystem health” to provide an ecosystem’s health history (4). Some taxa in paleoecological records are “indicators” of particular ecological conditions that can provide useful “symptoms” about the ecosystem’s health. Paleolimnologists (4) have effectively applied the concept of ecosystem health to lakes in relation to critical loads of pollutants. The same concept could be usefully applied to forests, heathlands, grasslands, wetlands, tundra, and savannas.

4) Greater discussion and collaboration between paleoecologists and conservation biologists, so that the most pertinent and urgent research questions are addressed together and the most relevant paleoecological data are collected at the spatial and temporal scales of direct concern in conservation.

Paleoecology provides a historical perspective that can help put present and future conservation and management policies into context. The time is ripe for the two disciplines to work more closely together and to develop a common agenda for biodiversity conservation.

References and Notes

- National Research Council, *The Geological Record of Ecological Dynamics: Understanding the Biotic Effects of Future Environmental Change* (National Academies Press, Washington, DC, 2005).
- L. Graümlich, S. Sugita, L. B. Brubaker, V. M. Card, *Ecology* **86**, 1667 (2005).
- K. J. Willis, L. Gillson, T. Brncic, B. Figueroa-Rangel, *Trends Ecol. Evol.* **20**, 107 (2005).
- J. P. Smol, *Pollution of Lakes and Rivers—A Paleoenvironmental Approach* (Arnold, London, 2002).
- H. J. B. Birks, *Grana* **44**, 1 (2005).
- M. E. Lyford, S. T. Jackson, J. L. Betancourt, S. T. Gray, *Ecol. Monogr.* **73**, 567 (2003).
- S. T. Gray, J. L. Betancourt, S. T. Jackson, R. G. Eddy, *Ecology* **87**, 1124 (2006).
- H. J. B. Birks, *J. Veg. Sci.* **7**, 89 (1996).
- P. B. Landres, P. Morgan, F. J. Swanson, *Ecol. Appl.* **9**, 1179 (1999).
- T. W. Swetnam, C. D. Allen, J. L. Betancourt, *Ecol. Appl.* **9**, 1189 (1999).
- L. Gillson, K. J. Willis, *Ecol. Lett.* **7**, 990 (2004).
- D. R. Foster *et al.*, *Bioscience* **53**, 77 (2003).
- G. M. MacDonald, *Adv. Ecol. Res.* **24**, 67 (1993).
- S. T. Jackson, in *Assessment and Management of Plant Invasions*, J. O. Luken, J. W. Thieret, Eds. (Springer-Verlag, New York, 1997), p. 37.
- L. Hannah *et al.*, *Conserv. Biol.* **16**, 264 (2002).
- J. B. Callicott, *J. Biosci.* **27**, 409 (2002).
- J. Gurevitch, D. K. Padilla, *Trends Ecol. Evol.* **19**, 470 (2004).
- S. Henderson, T. E. Dawson, R. J. Whittaker, *Prog. Phys. Geogr.* **30**, 25 (2006).
- C. D. Preston, D. A. Pearman, A. R. Hall, *Bot. J. Linn. Soc.* **145**, 257 (2004).
- E. A. Lynch, K. Saltonsall, *Wetlands* **22**, 637 (2002).
- J. F. N. Van Leeuwen *et al.*, *Neobiota* **6**, 27 (2005).
- V. S. Johnson, J. A. Litvaitis, T. D. Lee, S. D. Frey, *For. Ecol. Manage.* **228**, 124 (2006).
- D. F. Sax, J. H. Brown, *Glob. Ecol. Biogeogr.* **9**, 363 (2000).
- B. Von Holle, H. R. Delcourt, D. Simberloff, *J. Veg. Sci.* **14**, 425 (2003).
- C. I. Millar, W. B. Woolfendon, *Ecol. Appl.* **9**, 1207 (1999).
- W. J. Bond, J. E. Keeley, *Trends Ecol. Evol.* **20**, 387 (2005).
- D. McKenzie, Z. Gedalof, D. L. Peterson, P. Mote, *Conserv. Biol.* **18**, 890 (2004).
- P. Z. Fulé, W. W. Covington, M. M. Moore, *Ecol. Appl.* **7**, 895 (1997).
- C. Whitlock, *Nature* **432**, 28 (2004).
- J. A. Lynch, J. L. Hollis, F. Sheng Hu, *J. Ecol.* **92**, 477 (2004).
- K. J. Brown *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 8865 (2005).
- J. S. Clark, P. D. Royall, C. Chumbley, *Ecology* **77**, 2148 (1996).
- J. S. Clark, E. C. Grimm, J. Lynch, P. G. Mueller, *Ecology* **82**, 620 (2001).
- A. L. Maxwell, *J. Biogeogr.* **31**, 225 (2004).
- M. Lindbladh, M. Niklasson, S. G. Nilsson, *Biol. Conserv.* **114**, 231 (2003).
- L. Hannah, G. F. Midgley, D. Millar, *Glob. Ecol. Biogeogr.* **11**, 485 (2002).
- M. B. Araújo, M. Cabeza, W. Thuiller, L. Hannah, P. H. Williams, *Glob. Change Biol.* **10**, 1618 (2004).
- C. D. Thomas *et al.*, *Nature* **427**, 145 (2004).
- E. Martínez-Meyer, A. Townsend Peterson, W. W. Hargrove, *Glob. Ecol. Biogeogr.* **13**, 305 (2004).
- M. B. Araújo, C. Rahbek, *Science* **313**, 1396 (2006).
- FAUNMAP Working Group, *Illinois State Mus. Sci. Pap.* **25** (1994).
- E. Martínez-Meyer, A. Townsend Peterson, *J. Biogeogr.* **33**, 1779 (2006).
- R. H. W. Bradshaw, M. Lindbladh, *Ecology* **86**, 1679 (2005).
- A. Hampe, R. J. Petit, *Ecol. Lett.* **8**, 461 (2005).
- D. Jablonski, *Nature* **427**, 589 (2004).
- K. D. Bennett, P. C. Tzedakis, K. J. Willis, *J. Biogeogr.* **18**, 103 (1991).
- P. C. Tzedakis, I. T. Lawson, M. R. Frogley, G. M. Hewitt, R. C. Preece, *Science* **297**, 2044 (2002).
- K. J. Willis, J. C. McElwain, *The Evolution of Plants* (Oxford Univ. Press, Oxford, 2002).
- O. Duriez *et al.*, *Conserv. Genet.*, in press.
- M. E. Douglas, M. R. Douglas, G. W. Schuett, L. W. Porras, *Mol. Ecol.* **15**, 3353 (2006).
- L. Gillson, K. I. Duffin, *Philos. Trans. R. Soc. London Ser. B*, in press.
- M. A. Reid, R. W. Ogden, *River Res. Appl.* **22**, 167 (2006).
- M. Kowalewski, G. E. A. Serrano, K. Flessa, G. A. Goodfriend, *Geology* **28**, 1059 (2000).
- S. T. Dunn, *Alien Flora of Britain* (West Newman, London, 1905).
- A. R. Clapham, T. G. Tutin, E. F. Warburg, *Flora of the British Isles* (Cambridge Univ. Press, Cambridge, 1952).
- C. A. Stace, *New Flora of the British Isles* (Cambridge Univ. Press, Cambridge, 1991).
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