AFRICAN PLANT DIVERSITY AND CLIMATE CHANGE

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ABSTRACT

International goals have been set to protect global plant diversity and limit ecosystem damage due to climate change, but large-scale effects of changing climate on species distributions have yet to be fully considered in conservation efforts. For sub-Saharan Africa we study the shifts in climatically suitable areas for 5197 African plant species under future climate models for the years 2025, 2055, and 2085 generated by the Hadley Center's third generation coupled ocean-atmosphere General Circulation Model. We use three species distribution models, a "Box model," a simple genetic algorithm, and a Bayes-based genetic algorithm. The results show major shifts in areas suitable for most species with large geographical changes in species composition. The areas of suitable climate for 81%–97% of the 5197 African plant species are projected to decrease in size and/or shift in location, many to higher altitudes, and 25%–42% are projected to lose all of their area by 2085. In particular, the models indicate dramatic change in the Guineo-Congolian forests, mirroring proposed ecological dynamics in the past. Although these models are preliminary and may overestimate potential extinctions, they suggest that efforts to protect African plant diversity should take future climate-forced distribution changes into account.

Key words: Africa, biodiversity, climate change, conservation, extinction, Global Strategy for Plant Conservation (GSPC), Important Plant Areas.

Biodiversity conservation is typically implemented by delimiting a piece of land as a site of special scientific interest, nature reserve, or national park. This has the advantage of permitting a set of management criteria to be applied to a clearly defined area with discrete boundaries and can be used to preserve both particular types of ecosystems and rare organisms. Alternatively, certain species can be protected by creating a list of key taxa, such as Red Lists (Baillie et al., 2004) or species appended to the Convention on International Trade in Endangered Species (Ong, 1998), that have a legal status that prevents them from being interfered with even though they might occur outside areas designated for nature conservation. This is useful for uncommon taxa with a wide range, migratory species, and plants and animals of special significance. However, climate change may result in significant distributional shifts of entire ecosystems, and the creation of novel community associations as species respond to new conditions in an individualistic manner. This might make existing networks of protected areas redundant and lists of legally protected taxa inadequate. The prospect of increased climate dynamics has led to a proposal for "climate change-integrated conservation strategies," the first step of which is to undertake regional modeling of biodiversity response to climate change (Hannah et al., 2002b: 265).

Plant conservation has recently been given a major boost with the creation of the Global Strategy for Plant Conservation (GSPC) by the sixth meeting of the conference of the parties to the Convention on Biological Diversity (CBD) held in The Hague in April 2002 (Convention on Biological Diversity, 2002). Arising from the keynote address by Peter Raven to the 1999 International Botanical Congress in St. Louis, Missouri, which called for efforts to save the 300,000 kinds of plants in the world (Raven, 2004: 103), the primary objective of the GSPC is *"to halt the current and continuing loss of plant diversity"* (Convention on Biological Diversity, 2002: 3), which it aims to do by meeting 16 targets by the year 2010. Target five is *"Protection of 50 per cent of the most important areas for plant diversity assured"* (Convention on Biological Diversity, 2002: 7), giving rise to the concept of Important Plant Areas as a conservation tool (Anderson, 2002; Plantlife, 2004). The first steps to establishing the criteria needed to draw up a list of Important Plant Areas for Africa were taken at meeting of the Southern African Botanical Diversity Network (SABONET) in Pretoria 10–14 May 2004 (Lovett, 2004; SABONET, 2004; Smith & Smith, 2004).

Here, we consider the effects of projected climate changes on continental-scale distribution of African plant species, changes that have important implications for nations attempting to meet the GSPC targets, especially since Africa is thought to be the continent most vulnerable to climate change (IPCC, 2001). We conclude that climate change over the next 50 to 80 years, under current greenhouse gas emissions scenarios, will have a major impact on the location and nature of African plant diversity and needs to be taken into account when defining Important Plant Areas.

METHODS

SPECIES DATA

Since 2003 data on Africa-wide plant distributions have been contributed by various research institutions to a Biogeographic Information System on African Plant Diversity (BISAP), which is hosted and curated at the Nees Institute for Biodiversity of Plants (BIOMAPS project within the BIOLOG BIOTA framework). The data have been used for a variety of analyses of African plant diversity (Lovett et al., 2000; La Ferla et al., 2002; Taplin & Lovett, 2003; Burgess et al., in press; Küper et al., 2004; Linder et al., 2005). Examples of distribution patterns can be seen on the Centre for Ecology, Law and Policy (2004) plant mapping website <http://www.york.ac.uk/res/celp/webpages/projects/worldmap/worldmap.htm>.

The species database includes over 6200 taxonomically revised species with more than 330,000 distribution records from confirmed collection localities. Requests for information concerning the plant distribution database should be directed to Wolfgang Küper (e-mail address: wk@uni-bonn.de). For this study, only the 5197 species occurring on the African mainland south of latitude 27°N with distribution records in at least two grid cells have been considered: a total of 93,715 one-degree grid cell records. The sample accounts for between 10% and 15% of the African flora (Beentje et al., 1994) and 1.6% of the world's plant species (Barthlott et al., 1999; Prance et al., 2000). Plant distribution data from north of latitude 27°N are too sparse for the purposes of modeling. Spatial resolution of the plant distribution data used here varies between point data, mainly from herbarium collections with georeferenced localities, to 1° resolution data from digitized maps. All distribution data were rescaled to a one-degree latitude-longitude grid. Although these are the most comprehensive data ever assembled for the study area, many species may occur in more than the currently documented grid cells, a

Table 1. The climate variables used for all models.

Variable name	Variable description
MTW	Mean temperature of the warmest month
MTC	Mean temperature of the coldest month
ATR	Annual range of mean monthly temperature
MINTC	Mean minimum temperature of coldest month
MAXTC	Mean maximum temperature of warmest month
AMIN	Absolute minimum temperature
MAP	Mean annual precipitation
MAPD	Mean annual precipitation of the driest month
AMI	Annual moisture index

problem inherent in most biogeographic data sets (Williams et al., 1996).

CLIMATE DATA

Climate predictions are from the Hadley Centre's third generation coupled ocean-atmosphere General Circulation Model, HadCM3B1 (The Climate Impacts LINK Project, 2004 <http://www.cru.uea.ac.uk/link/new_link/welcome.html>). The B1 scenario has been developed by the IPCC (Nakićenović & Swart, 2000) and describes the most conservative estimate of climate change from the HadCM3 output. Climate scenarios were developed around the four time periods of 1975, 2025, 2055, and 2085 based on 30-year averages. Data representing an average around the year 1975 were used as present climate variables on which to base each species model. The GCM data are provided at a global scale in a non-regular 2.5 × 3.75 degree grid structure. In order to maintain consistency with the regular 1-degree resolution of the continental-scale plant species data, the GCM data were converted to lattices of points from which 1 × 1 degree continuous surfaces were interpolated (Carter et al., 1999) using a simple inverse distance weighting method using the eight nearest neighbors. The variables used in the continental scale modeling are given in Table 1. Absolute minimum temperature was calculated following Prentice et al. (1992). Annual moisture index is the quotient between mean annual precipitation and mean annual potential-evapotranspiration. The latter was calculated using the Thornthwaite equation (Stephenson, 1998) incorporating a latitude-based estimate of day length (Forsythe et al., 1995). The elevation data used in the study were the GTOPO30, 30 arc-second gridded digital elevation model for the globe (Land Pro-

cesses Distributed Active Archive Archive Center, 2004 <http://edcdaac.usgs.gov/gtopo30/gtopo30.asp>).

MODELING

We used distribution modeling that matches the location of observed species occurrence records with the spatial partitioning of appropriate climate variables. These types of models have also been variously described as niche models and bioclimatic envelopes (MacArthur, 1972; Huntley et al., 1995; Pearson et al., 2002; Peterson et al., 2002; Pearson & Dawson, 2003). In order to evaluate the sensitivity of our biological conclusions to methodological details we used three distribution model variants derived from currently available methods. The first (BOX) is similar to a "Box model" (Box, 1981), which represents the full range (extremes) of climate space a species is observed to inhabit. The second method attempts to find the environmental range that maximizes the number of correctly predicted occurrences while minimizing overprediction of species presence using a simple genetic algorithm (SGA). The third method, a Bayes-based genetic algorithm (BGA), calculates the probability of occurrence for a species given a set of climatic variable thresholds using a Bayesian classifier and a genetic algorithm. We assume either full dispersal or no dispersal (Peterson et al., 2002; Thomas et al., 2004a). Full dispersal assumes that species can disperse from one location in Africa to any other location irrespective of distance; no dispersal assumes that species cannot disperse to other grid cells. Once we have modeled a species using current climate spatial distributions, we can observe where the climate would be expected to be suitable for the species under future climate predictions.

Ideally, from a modeling perspective, all species would have a large number of presence observations, as this would allow species data to be split into calibration and validation data sets that could be used to test the predictive accuracy of the models. However, Stockwell and Peterson (2002) demonstrated the problem associated with not including data: accuracy of models appears to increase as more observations are included. This would become a major issue when analyzing plants with a small number of observations. We have, therefore, used all available records for each species. Not doing so could result in us missing out observations that give important information about the current climate conditions in which the plant is found. The three modeling techniques are described in more detail

below. The three different algorithms were coded in "C" and input-data stored as ascii files in ESRI's Grid format. Spatial data handling prior to running the models, as well as the handling of spatial results, was performed using the GRASS 5.3 GIS software <http://grass.itc.it>). Cartographic output was produced using ArcView 3.3.

THE BOX MODEL

For the BOX model each species distribution record is overlain with each climate variable in turn. For each climate variable, the maximum and the minimum values found at the location of the distribution records are recorded. Nine climate surfaces are used in the analysis, and these define a nine-dimensional climate envelope. If the areas falling within each of the ranges given by the nine minimum and maximum values for the nine climate surfaces are mapped, this provides an indication of all the areas that might be climatically suitable for the species. All the species presence observations will be contained within this mapped envelope, but so too will many areas without a distribution record. The BOX model therefore tends to overpredict species occurrences. No weights are given to the various climate thresholds that might be most important to the species; in this way a future climate change in any one of the variables used to produce the model can result in areas that were previously climatically suitable being deemed as climatically unsuitable. Adaptations of this method have been used in a number of previous studies (Box et al., 1993, 1999; Crumpacker et al., 2001). To assess the fit of predicted to observed patterns of individual species models, we use the kappa coefficient, which attempts to balance the assessment of errors of both omission and commission resulting from the model (Manel et al., 2001). Based on the confusion matrix produced by comparing two classifications, in our case a simple cross-tabulation of observed presence/absence with predicted presence/absence, this coefficient can take a value from 0, complete disagreement between predicted and observed, to 1, complete agreement between predicted and observed. Kappa was calculated using observed and predicted presence/absence maps in GRASS 5.3.

GENETIC ALGORITHMS

The genetic algorithms (GA) seek to identify the distribution of climate variables that give the closest match to the observed species presence patterns. Both GA approaches used in this study share the basic approach behind all genetic algorithms;

in the context of bioclimatic modeling these are as follows.

The genetic algorithm starts with a "population" of possible climate variable ranges, known as "chromosomes." These ranges are obtained by taking subsections of the full ranges that occur in the study area. One possible chromosome is the set of ranges used in the BOX model. Another example would be a chromosome from the population that has a minimum value for mean maximum temperature of the warmest month of 25°C, a maximum value for mean maximum temperature of the warmest month of 32°C, a minimum value for mean annual precipitation of 600 mm, a maximum value for mean annual precipitation of 850 mm, and so on, until ranges are defined for each of the climate variables included in the analysis. Each minimum or maximum value represents one "gene" on a chromosome. Genes are allocated randomly to the initial population from within the full climate variable ranges that occur in the study area. The areas accounted for by the set of variable thresholds contained in the genes of a chromosome can be mapped and compared to the observed distribution. A score can be calculated to measure how well that chromosome captures the observed plant distribution. Continuing the natural selection analogy, this score is described as the fitness of the chromosome.

On the basis of their fitness values, members of the population are allowed to reproduce. If a chromosome has a high fitness score, it has a higher probability of reproducing with another chromosome from the population. Reproduction occurs by taking a number of genes from one chromosome and a number of genes from the other chromosome. This is analogous to the biological phenomenon of crossover, in which two offspring chromosomes are produced. In this way genes that provide good solutions are taken from successful individuals into the next generation in a search for the optimal solution. However, the genes of the initial population may not be the genes that can provide the best possible fit between the climate variables and the observed species distribution. In an attempt to avoid local maxima resulting from the limited nature of the genes of the initial population, an operation known as mutation is added to the algorithm. A mutation operation simply allows the value of a randomly selected gene on a randomly selected chromosome to be changed by a random number. Mutations can survive into future generations if the fitness scores of the mutated chromosomes are high enough to allow them to reproduce. The algorithm advances through generations of solutions until no noticeable improvements are made to the fitness

score of the fittest chromosome. The difference between the Simple Genetic Algorithm (SGA) and Bayes-based Genetic Algorithm (BGA) models used here is the measure of fit used to assess how well the pattern predicted by a chromosome fits the observed species presence pattern, which is termed the fitness score.

SIMPLE GENETIC ALGORITHM (SGA) MODEL

The fitness score used in this method is Dice's or Sørensen's index (Krebs, 1999). This compares the number of correct predictions with the number of overpredictions as follows:

$$ s = \frac{2a}{a + b + c} $$

where s is Sørensen's index; a is the number of correct predictions; b is the number of false positives; c is the actual number of presence observations. If the number of correct predictions equals the number of actual presence observations, the number of overpredictions is zero and the index will equal one.

The effect of using this index as the fitness score measure for chromosomes in the GA is that observed species presences are traded off against overpredictions. So observations on the edge of the BOX model can be left out of the solution allowing narrower thresholds within the climate ranges to be found. In this way the SGA approach can be more sensitive to the variables that constrain the model most. Once again, in future time periods if a location falls outside the thresholds found for any of the climate variables used to determine the model, the location will be deemed to have climate unsuitable for the species. As with the BOX models, the quality of SGA model results were also assessed using the kappa coefficient.

BAYES-BASED GENETIC ALGORITHM (BGA)

The fitness score used in this method involves Bayes's theorem and is based on predictive modeling approaches using Geographical Information Systems (GIS) (Aspinall, 1992; Tucker et al., 1997). Bayes's theorem in this application can be stated as follows:

$$ P(Y | X_1 \cap X_2 \cap X_3 \cdots X_n) $$

$$ = \frac{P(Y) \prod_{i=1}^{n} P(X_i | Y)}{P(Y) \prod_{i=1}^{n} P(X_i | Y) + P(notY) \prod_{i=1}^{n} P(X_i | notY)} $$

where event Y is the presence of a species and $notY$

Table 2. Frequency with which climate variables are found to be the most important model variables (BGA method).

Variable name	Frequency	Percentage	Cumulative percent
MAP	1022	19.7	19.7
MTW	822	15.8	35.5
AMI	760	14.6	50.1
MAXTC	562	10.8	60.9
ATR	507	9.8	70.7
MAPD	479	9.2	79.9
AMIN	374	7.2	87.1
MINTC	350	6.7	93.8
MTC	321	6.2	100

is the absence of a species, X_i is the presence of a climate variable, i, within certain minimum/maximum thresholds. The left-hand side of the equation is the probability of the event that a species is present given the occurrence of the set of n climate variable thresholds (known as the posterior probability). For each chromosome in the GA, the minimum, maximum gene couplets represent the X_i. Within a raster- or point-based GIS environment, the $P(X_i | Y)$ and $P(X_i | notY)$ terms can be calculated by counting the pixels/points between the minimum and maximum values provided by the genes that occur where the species is present (Y) or absent ($notY$). By using the formula for the combination of climate variable ranges, given by a chromosome, for each pixel/point we obtain a posterior probability of finding the species. These maps of posterior probability can then be analyzed to produce the final fitness score: the difference between the average probability for pixels/points with the species and the average probability for pixels/points without the species. In this case the GA's solution to maximizing the fitness score settles on the climate variable ranges that separate presence and absence pixels/points. By studying the magnitude of the difference between the $P(X_i | Y)$ and $P(X_i | notY)$ terms for the best chromosome obtained by the GA, we can interpret which factors have most influence on the final posterior probability scores and therefore which climate variables appear most important to the species. For the species studied here, the number of times each climate variable is found to be most important to the model definition is recorded in Table 2. The predictive ability of models based on presence/absence data, where estimates of the probability of occurrence for each observation are provided, can be assessed by constructing the relative operating characteristics curve (ROC). The area under this curve (AUC) pro-

vides the assessment of the predictive abilities of the model (Pearce & Ferrier, 2000). This value can vary from 0.5, the model has no predictive ability, to 1, perfect ability to predict. We calculate the AUC score for each species model when using the BGA approach.

CALCULATING ELEVATION DATA FOR CLIMATE MODEL PREDICTIONS

From the original 30 arc second raster data, the median elevation of each one-degree grid cell in the African study area was calculated. For each individual species in the BOX and SGA model results, the average of the one-degree median elevation values was calculated for cells that were predicted to contain suitable climate. For the BGA model, probability of suitable climate occurrence was used to calculate a weighted mean elevation for each species model.

CALCULATING FLORISTIC TURNOVER FOR EACH GRID CELL

Dice's or Sørensen's index was used to assess the amount of change between present and future periods in each one-degree cell:

$$s = \frac{2a}{a + b + c}$$

where a is now the number/level of probability of species with suitable climate found in a cell for both the future period and the present; b is the number/level of probability of species with suitable climate entering a cell in the future, but not found in the present model; c is the number/level of probability of species with suitable climate found in the present period. If all species with suitable climate found in the present period are also found in the future period and there are no additional species, the index will have the value one.

CALCULATING AVERAGE CLIMATE VARIABLE VALUES FOR SPECIES PRESENT PREDICTIONS

It is difficult to obtain a measure of how particular changes in individual climate variables will affect plant diversity across Africa because of the multidimensional nature of the climate spaces we consider. We can, however, consider how these variables are predicted to change over the study periods in the geographical areas that currently have suitable climate for the species. To do this for the BOX and SGA models of each individual species, the average of each climate variable was calculated for cells that were predicted to contain suitable cli-

mate in the present period; for the same cells, these statistics were calculated for each of the future periods. For the BGA model the probability of suitable climate occurrence was used to calculate a weighted mean for each species' model. Examples of the distributions obtained for a temperature and a precipitation variable are given in Figures 1 and 2.

RESULTS

For each modeling approach and for each one-degree grid cell, summing across model predictions for each species allows an assessment of the number of species bioclimatic envelopes that are suited to the environment of a cell. Comparison of these summations with the number of species actually observed in each grid cell (species richness) demonstrates that areas of suitable contemporary climate for varying numbers of species are well correlated with observed species richness for the SGA and BGA models ($r_s = 0.75$ and 0.73, respectively), while the BOX model is less well correlated ($r_s = 0.52$) because this climate distribution model includes the most extreme climate variable values found for each species. These overall patterns are in agreement with the assessments of individual model performance. The BOX models have a symmetrical distribution of kappa coefficients with a mean value of 0.548 and a standard deviation of 0.332. The SGA model results have a negatively skewed distribution of kappa coefficients with a median value of 0.716 and an interquartile range of 0.358. Three-quarters of the models have a value above 0.530. The distribution of BGA model AUC scores is negatively skewed with a short tail of poor AUC scores. The median AUC score is 0.971 with an interquartile range of only 0.098. Only 61 of the models give an AUC score of less than 0.75.

By 2085, models show that between 81% and 97% of species have lost areas of suitable climate across the study area (Table 3). Species losing some area of suitable climate greatly outnumber species gaining area of suitable climate (using the full dispersal assumption) in all scenarios and for all models. Loss in area of suitable climate for individual species is most pronounced under the BOX and SGA models, because these models deem a cell unsuitable if even one future climate variable value for the cell falls outside the modeled climate niche of the species. The BGA model allows the probability of occurrence of climatic suitability to be reduced as climate changes, rather than predicting complete unsuitability. As a result, it provides consistently lower estimates of change when these probabilities are summed across Africa.
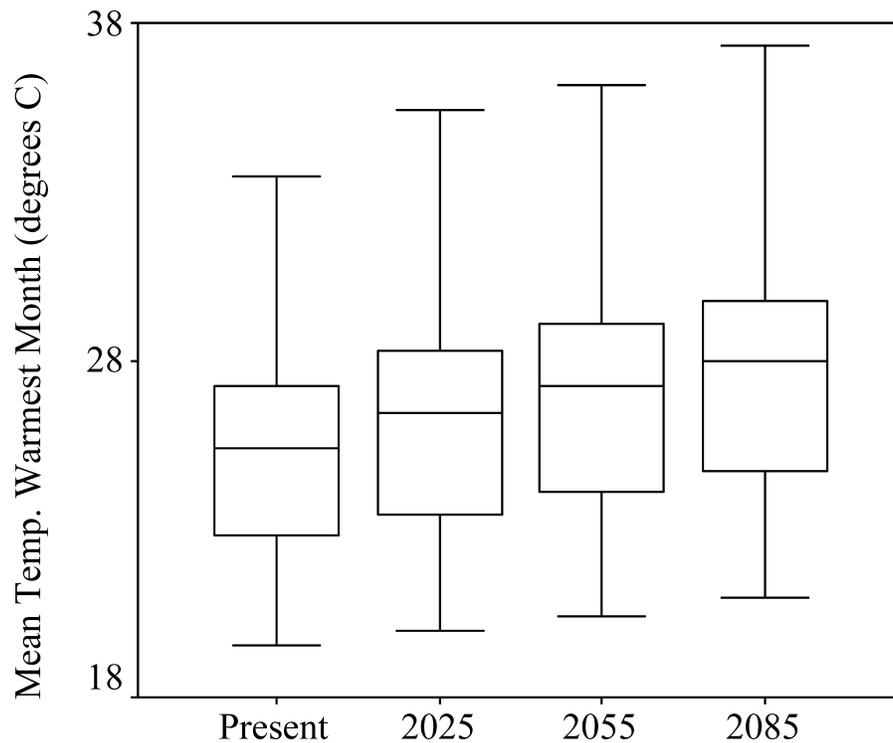
Figure 1. Box-plots of the mean temperature of the warmest month for grid cells detected as areas of suitable climate for each species under current predictions. Middle line in boxes gives median value for 5197 species. Upper line of box gives upper quartile, while lower line gives lower quartile. Whiskers extend over range after outliers and extremes have been removed. These results are for the BGA model.

Extinction risk may be estimated by the number of species that lose all suitable climate in a future scenario. Total loss of all area of suitable climate is projected for 25%–57% of species by 2085 under the full dispersal assumption and 34%–76% if no dispersal is assumed. Some 19% (full dispersal) to 28% (no dispersal) of our sample species are projected to lose all areas of climate suitability by 2055, in our conservative BGA model. The values are higher than estimates of 4%–19% of species projected to lose all of their suitable climate space by 2050 in a recent study (Thomas et al., 2004a, b), but for the most part lower than the 15%–37% (mid-range climate scenario) of species predicted to become extinct in the long run by the methods of the same study that extrapolate extinction risk for species with reduced areas. Adopting the latter methods would increase our estimates of extinction risk in all scenarios and models. Importantly, by 2085 even our most conservative model and dispersal assumptions project that 25% of species will lose all of their climatically suitable area, close to the predicted long-term extinction levels estimated by Thomas et al. (2004a) for climate change by 2050.

To estimate the geographic distribution of these changes under the assumption of full dispersal, we calculated the percentage change in the number of species for which a grid cell is predicted to be climatically suitable between present and future periods (Fig. 3a–i). This gives a view of the dynamics of changing areas of climate suitability across time. The three models agree on a number of trends. Many species lose climatically suitable areas from "hotspots," which are already recognized as centers of high biodiversity under severe threat (Myers et al., 2000; Küper et al., 2004). All models show progressive loss of areas of suitable climate for species in the Guineo-Congolian rain forests of West and Central Africa, including the central Congo Basin, accompanied by gains in surrounding uplands. Other highland areas such as the Drakensberg Mountains and Namibian Highlands also potentially provide areas of suitable climate for many species new to these regions. In eastern Africa, the Eastern Arc and Coastal Forests of Tanzania and
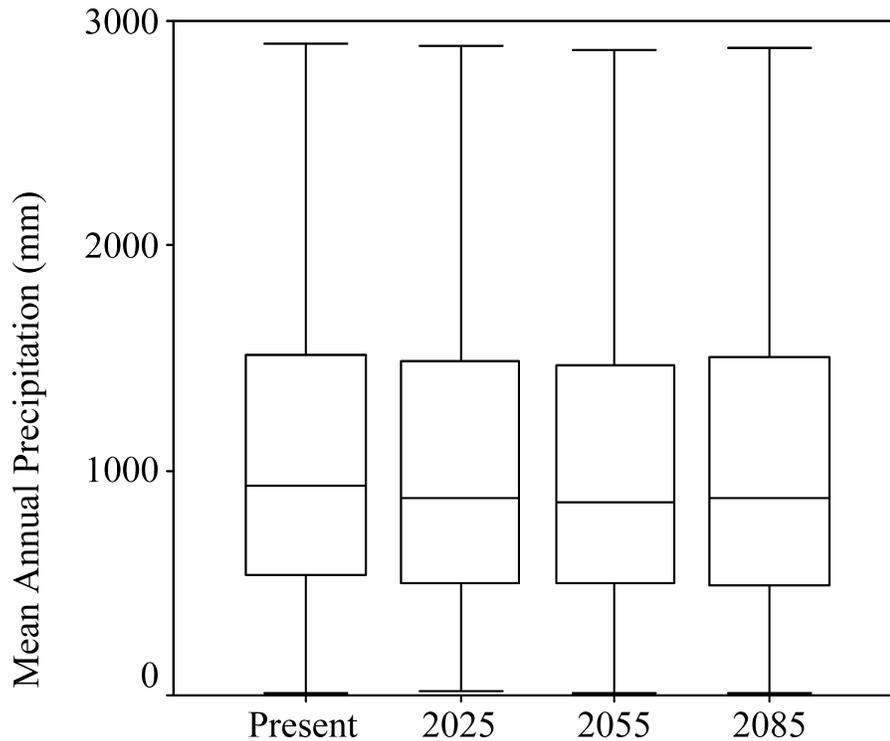
Figure 2.   Box-plots of mean annual precipitation for grid cells detected as areas of suitable climate for each species under current predictions. Middle line in boxes gives median value for 5197 species. Upper line of box gives upper quartile, while lower line gives lower quartile. Whiskers extend over range after outliers and extremes have been removed. These results are for the BGA model.

Kenya begin to lose climatically suitable areas by 2025 in the SGA and BGA models (Fig. 3d, g). By 2085 the Western African Forests and the Succulent Karoo have lost much of their suitability for many species.

For the present predictions and the three future periods' predictions (full dispersal) we have cal-culated the average altitudes of the grid cells that contain suitable climate for each species. These av-erage altitudes increase over each of the time pe-riods modeled (Table 3, Fig. 4). The median alti-tude for species in 2085, for the conservative BGA model, is 178 m higher than the median for current predictions. However, even with full dispersal, spe-

Table 3.   Numbers of species out of 5197 (percentages given in parentheses) predicted to increase and decrease climatically suitable area (full dispersal assumption) and lose all climatically suitable area (under two dispersal as-sumptions). The final row records the change in the median value of average elevations for climatically suitable areas from present predictions.

|	BOX 2025	BOX 2055	BOX 2085	SGA 2025	SGA 2055	SGA 2085	BGA 2025	BGA 2055	BGA 285
Increasing climate suitability	616 (12%)	309 (6%)	146 (3%)	911 (18%)	571 (11%)	425 (8%)	1406 (27%)	1211 (23%)	994 (19%)
Decreasing climate suitability	4514 (87%)	4860 (94%)	5021 (97%)	4104 (79%)	4516 (87%)	4675 (90%)	3790 (73%)	3986 (77%)	4202 (81%)
Area lost (no dispersal)	1696 (33%)	2424 (47%)	2891 (56%)	2572 (49%)	3498 (67%)	3955 (76%)	1073 (21%)	1437 (28%)	1752 (34%)
Area lost (full dispersal)	1341 (26%)	1855 (36%)	2185 (42%)	1851 (36%)	2561 (49%)	2950 (57%)	768 (15%)	1007 (19%)	1298 (25%)
Increase in elevation (m)	152	239	343	173	294	390	111	137	178
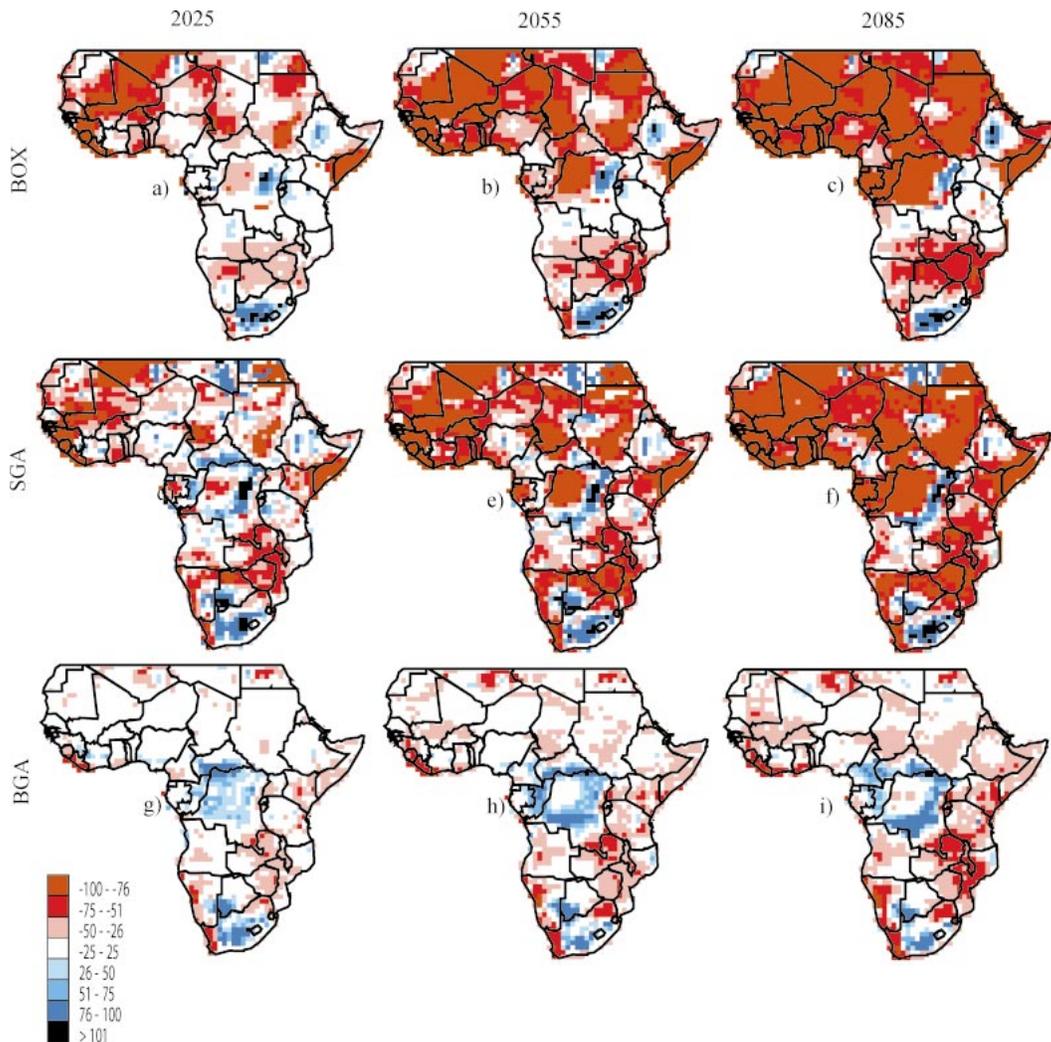
Figure 3.   Percentage change in the number of species for which one-degree cells are climatically suitable between present predictions and future predictions.

cies are limited by fixed upper limits to elevation across Africa, as is demonstrated by the interquartile range of species' average altitudes becoming reduced as the lower quartile value increases in line with the median, while the upper quartile increases only marginally in later periods (Fig. 4).

Important temperature variable thresholds may also be squeezed in this way. For the BGA model we can, however, ascertain which climate variables are most influential in determining which areas are most suitable for a species. Across all of the species we study, the three most influential variables are annual precipitation, mean temperature of the warmest month, and annual moisture index (19.7%, 15.8%, 14.6% of species, respectively; Tables 1, 2). Our study of the changes in the climate vari-

ables over the study periods in the geographical areas that currently have suitable climate for the species (Figs. 1, 2) shows that across the sample species, on average, temperature variable values rise while precipitation-based variable values fall. However, the precipitation variable decreases are much less pronounced than the temperature variable increases and the variations across the sample for precipitation variables tend to be larger. This indicates that there is both substantial geographical complexity in such changes and that increasing temperature variables are likely to be the driving factors behind the shift of climatically suitable areas to higher altitudes.

Finally, we calculate an index of floristic turnover for each grid cell. For future climate predic-
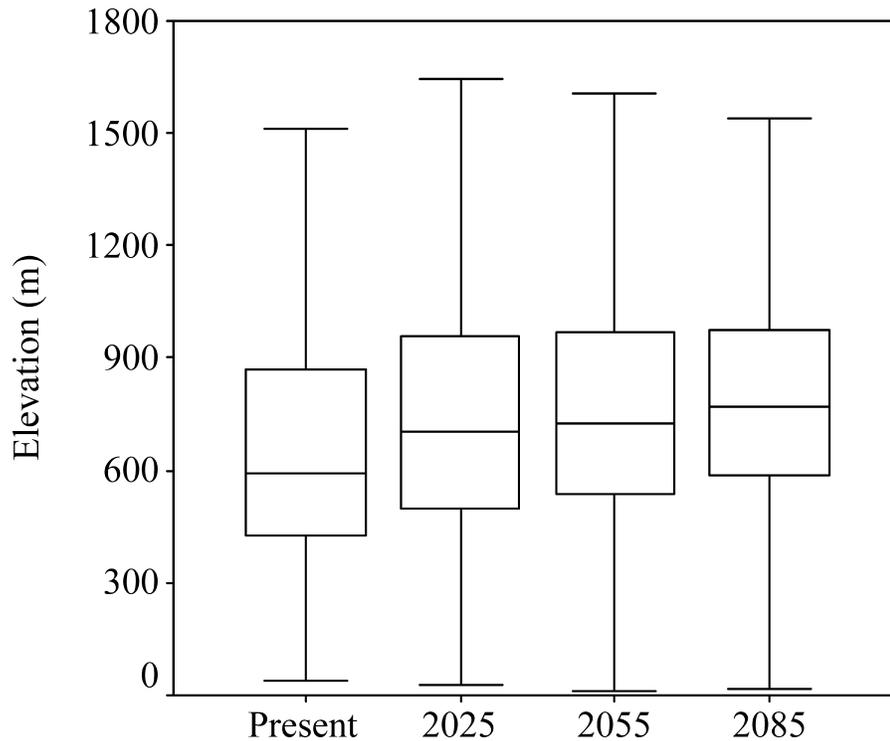
Figure 4. Box-plots of average elevation for climatically suitable areas for species in the four modeled time periods. Middle line in boxes gives median value for 5197 species. Upper line of box gives upper quartile, while lower line gives lower quartile. Whiskers extend over range after outliers and extremes have been removed. These results are for the BGA model.

tions, this takes into account how many species are left with suitable climate in a grid cell in relation to both the original number of species with suitable climate in that cell, and the number of species for which the cell becomes climatically suitable. A score of one suggests that there has been no change in the species for which the area is climatically suitable. A score of zero suggests that the area is no longer suitable for any of the original species. By 2085, most areas have an index of 0.5 or below, indicating that many areas have climate suitable for less than half the original species for which those areas were once suitable (Fig. 5a–i).

DISCUSSION

In the discussion we first address shortcomings of the modeling methodology, in particular the risk of overemphasizing extinction rates. Second, we briefly review our findings in the context of past climate change, and finally we make suggestions that might be useful for implementation of the Global Strategy for Plant Conservation.

The modeling technique has two main limitations that may lead to an overestimation of the effects of

climate change. Firstly, we assume that the presence of a plant species is solely determined by climate. In reality, the distribution of many plant species is in addition determined by, for example, competition, soil-type, fire, and micro-climates within structured vegetation. If other factors are suitable, species may have broader climatic tolerances than indicated by our model. Secondly, we are working at a scale of one degree. There can be high habitat heterogeneity within a one-degree cell and plants can survive periods of climatic extremes in small refugia. For example, many rainforest plants also occur in riverine or groundwater forests outside areas of continuous forest. Thus, when interpreting the results, it must be borne in mind that the model is showing extinction of potential climate-space (Table 3) rather than actual species extinctions. However, the model may also underestimate extinctions by not including factors such as fire. Africa has a long history of fire, with increases in fire episodes during switches of climate from interglacial to glacial, with a marked increase in fire during the present interglacial that is attributed to human influence (Bird & Cali, 1998). Drought and
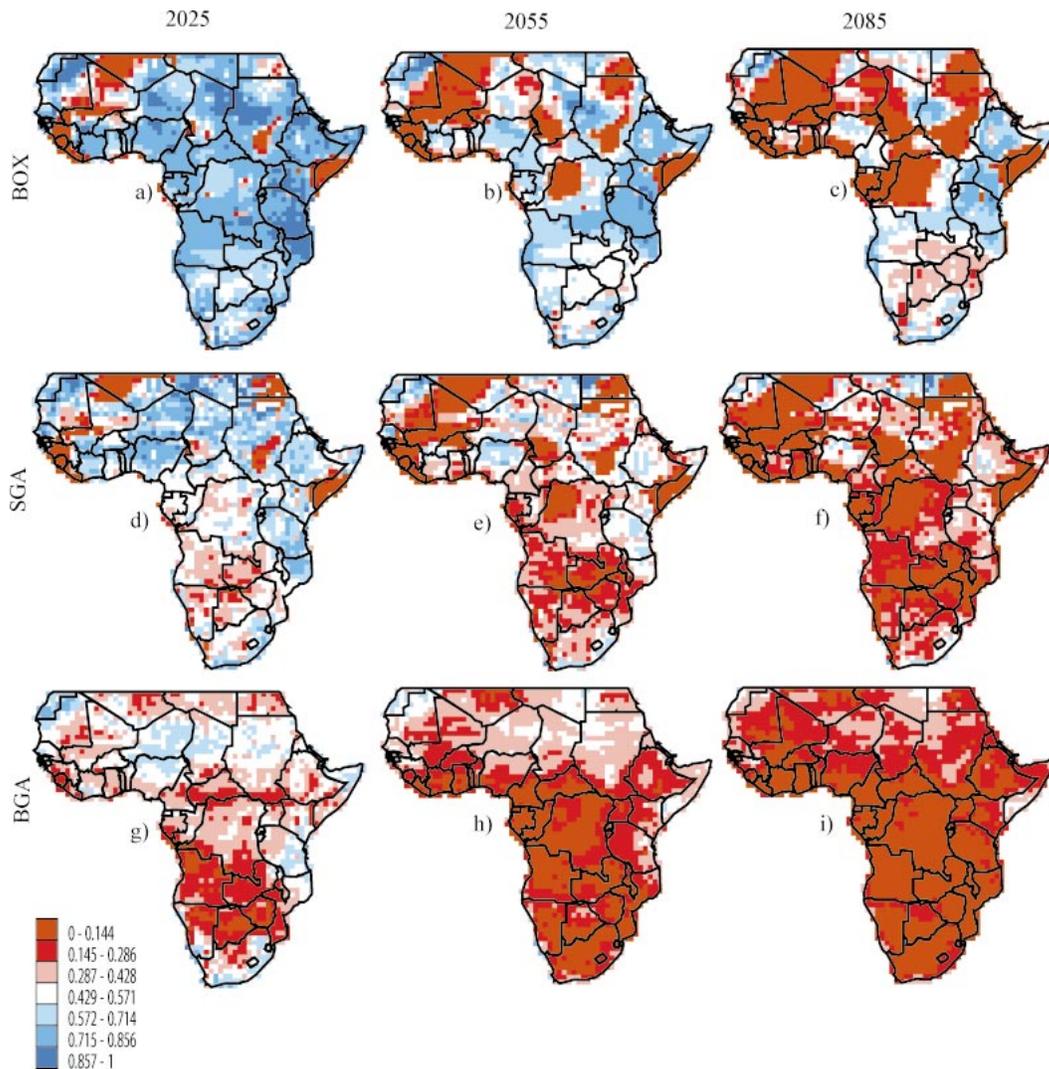
Figure 5.   Maps of Sørensen's index showing climate niche turnover from present predictions to future predictions.

disturbance are implicated in enhanced extinction rates in fire-vulnerable formations such as rainforests throughout the tropics (Nepstad et al., 1999; Taylor et al., 1999; Cochrane, 2003) including Africa (Clarke & Karoma, 2000), and fire is considered to be a major determinant of global vegetation patterns (Bond et al., 2005). The preliminary estimates presented here need much further investigation of species responses to climate variability in an ecosystem context, including the effects of disturbance and human impacts. For example, pioneer forest has expanded along the northern boundary of the Guineo-Congolian forests (J. Maley, pers. comm.), an observation that runs counter to the trends modeled here.

From the assessments of kappa coefficients for the BOX and SGA models, it appears that as expected, the simple genetic algorithm approach gives better discrimination in terms of correctly predicting species presence observations and minimizing overpredictions for present climate. When the climate thresholds found by these models are projected into future climates, these models are likely to be very strict in their assessment of where suitable climates for a particular species might be located. The resulting patterns of change reflect the severity of the assumptions in this modeling approach. However, the broader climate envelopes produced by the BOX models show the areas that possess the combinations of climate variables where species presence has been observed. When these envelopes are projected onto future climate,

we at least obtain the areas under future climate that have been observed to possess the species at present. The magnitude of change in these predictions is still dependent on the assumption that if suitability in terms of one climate variable is lost, all suitability is lost.

The BGA approach overcomes the latter assumption by allowing the probability of species occurrence to be reduced, but not removed, if an area becomes less suitable in terms of one (or more) climate variables. The high AUC scores associated with these models gives us some confidence that the influence associated with each climate variable in these models is sensibly apportioned, and therefore probabilities of occurrence in the future may be more robust than the simple presence/absence predictions of the other methods.

Despite limitations of the modeling technique, the results bear some similarities with proposed effects of past climate change. Dynamism of the Guineo-Congolian forests in our model is consistent with palaeoecological information, which suggests that Central and West Africa have been subject to large changes in climate, species composition, and species diversity (Servant et al., 1993; Maley, 1996; Maley & Brenac, 1998; Nichol, 1999). For example, range expansion of the oil palm (*Elaeis guineensis* Jacq.) is considered to be associated with late Holocene forest decline around 2500 yrs BP (Maley & Chepstow-Lusty, 2001), and genetic diversity of the shea tree (*Vitellaria paradoxa* C. F. Gaertn.) appears to be associated with climatic changes at the Dahomey Gap such as increased aridity and expansion of this arid corridor during the last glacial maximum 15,000–20,000 yrs BP (Fontaine et al., 2004).

Elevational range in the Drakensberg was picked out by our model as important as a potential refugium for plant survival. Modern-day plant diversity is associated with areas of high topodiversity (Mutke et al., 2002). A possible reason for this is that these areas offer an adjacent range of habitats within which plants can move during periods of climate change. African biodiversity hotspots may owe their existence to persistence in refugia through Quaternary climatic fluctuations, which were both cooler and drier than at present (Hamilton, 1976, 1982; Maley, 1991, 1996, 2001a) and warmer (at 2500 and 125,000 yrs BP, Maley, 1996, 2001b). In our model, despite high floristic turnover and loss of suitable climate for many species, the results show montane areas gaining in suitable climate space for many species. Similar effects may pertain at finer scales than that of this study (Hannah et al., 2002a; Midgley et al., 2003). This supports recent suggestions that areas of topographic diversity are likely to be important climate change refugia and so should, a priori, be selected for conservation (SABONET, 2004), following previous advocacy of such policies for specific areas in Africa (Cowling & Pressey, 2001; Cowling et al., 2003). Our results suggest that areas of high terrain diversity could provide useful additions to current in situ conservation efforts and be important for meeting the GSPC goals in the face of potential future climate change.

Microclimates at finer scales than that of this study may provide refugia for small populations of individual species, while the loss of broad-scale climate suitability indicated here will result in major loss of area of occupancy and population reductions. These results suggest that under pressures of climate change, species composition in areas may change quite drastically, with potentially profound effects on ecosystem stability and the associated ecosystem goods and services utilized by the human population. Beyond 2085, our results suggest that meeting existing conservation targets may no longer be possible if current greenhouse gas emission patterns continue unabated. This is not only relevant to the GSPC. Article 2 of the 1992 UN Framework Convention on Climate Change (UNFCCC) aims to reduce human-induced climate change to a level that will allow ecosystems to naturally adapt to climate change. Greater inter-agreement communication and greater recognition of the sensitivity of biodiversity to climate change seem necessary for both the CBD and UNFCCC to achieve their goals. Our work demonstrates that there may be great pressure on species to shift their ranges in response to changing environments. The rates at which species may be required to accomplish such shifts are likely to be determined by actions taken under the UNFCCC. Our results suggest that time is running out; climate change abatement strategies may be too slow to avoid many species losing major proportions of the areas that are climatically suitable for them. This and the associated potential changes in species composition have major implications for signatories to the CBD as they seek to establish systems of protected areas that will maintain plant species diversity.

In conclusion, we would like to emphasize the importance of primary data collection in the field. We are indebted to all those responsible for recording distribution data in monographs and preserving collections in herbaria. Our modeling work is dependent on such collections, and future recording efforts will continue to be essential for the successful implementation of the GSPC.

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