

Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance

Oren Farber, Ronen Kadmon *

Department of Evolution, Systematics and Ecology, Institute of Life Sciences, The Hebrew University, Givat-Ram, Jerusalem 91904, Israel

Received 10 January 2002; received in revised form 31 May 2002; accepted 2 October 2002

Abstract

We introduce the concept of the Mahalanobis distance to bioclimatic modeling. Specifically, we argue that climatic envelopes defined by the Mahalanobis distance produce more accurate predictions of species distribution than standard rectilinear envelopes (e.g. those produced by BIOCLIM). We base our hypothesis on three rationales: (1) the climatic envelope generated by the Mahalanobis distance is oblique, and therefore, may cope with correlations and interactions among the climatic variables; (2) the Mahalanobis envelope is elliptic, and therefore, better reflects the principle of central tendency as expressed by niche theory; (3) Mahalanobian predictions are based on the whole data rather than on the outermost observations, and are therefore, less sensitive to outliers. We test our hypothesis using data on the distribution of 192 species of woody plants in Israel. Validation tests based on four measures of accuracy (sensitivity, specificity, overall accuracy and the Kappa statistic) support our hypothesis, and suggest that Mahalanobis models produce predictions that are significantly more accurate than those produced by corresponding rectilinear models. Additional simulation experiments demonstrate that the superiority of Mahalanobian models cannot be related to their elliptic shape, or their ability to cope with correlations among the climatic variables. Accordingly, our conclusion is that the prime advantage of Mahalanobian models originates from the fact that their climatic envelopes are defined using all the observations, as opposed to rectilinear envelopes that are founded on the outermost observations.

© 2002 Elsevier Science B.V. All rights reserved.

Keywords: BIOCLIM; Climatic envelope models; Distribution range; GIS; Ecological niche; Kappa; Predictive maps

1. Introduction

Models predicting the distribution of organisms may contribute to our understanding of factors controlling patterns of species distribution, as well as for planning of conservation and management programs (Franklin, 1995; Iverson and Prasad, 1998; Bolliger et al., 2000; Godown and Peterson,

* Corresponding author. Tel.: +972-2-658-4305; fax: +972-2-658-4741.

E-mail address: kadmon@vms.huji.ac.il (R. Kadmon).

2000; Karl et al., 2000; Pearce and Ferrier, 2001). One class of predictive models that has been applied for a variety of scientific and practical purposes is termed climatic envelope models (CEMs). These models generate predictive maps of species distribution using data on the climatic characteristics of the sites where the species were recorded (Nix, 1986; Busby, 1986). CEMs involve two conceptual steps. The first step is the projection of the recording sites from the map into a multidimensional space defined by a set of climatic variables. The purpose of this step is to identify the climatic niche (also termed ‘climatic envelope’ or ‘climatic profile’) of the target species. The second step is the projection of the climatic niche from the multidimensional climatic space back into a two dimensional geographic space (i.e. a map). This step is also termed ‘homoclimate matching’ (Lindenmayer et al., 1991; Brereton et al., 1995) since a grid of the study area is scanned for locations with similar conditions to those of the species’ climatic profile.

CEMs have been applied for many purposes including the analysis of factors affecting distribution patterns of plants and animals (Walker and Cocks, 1991; Shao and Halpin, 1995), reconstruction of palaeoclimatic conditions and biogeographical processes (McKenzie and Busby, 1992; Kershaw, 1997), assessment of potential floristic and faunal responses to alternative scenarios of climate change (Brereton et al., 1995; Eeley et al., 1999), classification of wildlife habitats (Skidmore et al., 1996), exploration of potential areas for reintroduction of endangered species (Pearce and Lindenmayer, 1998), estimation of the spreading potential of pests and invasive plants (Honig et al., 1992; Sindel and Michael, 1992; Martin, 1996), identification of potential planting regions (Booth et al., 1988; Richardson and McMahon, 1992), and design of efficient field surveys (Lindenmayer et al., 1991). Most of these applications were carried out using the Australian software BIOCLIM (Nix, 1986; Busby, 1991). In addition to the enveloping algorithm, BIOCLIM provides comprehensive tools for climatic interpolation (Hutchinson, 1995), analysis of data integrity, and visualization.

The most important advantage of CEMs is their ability to cope with ‘presence only’ data (as opposed to presence–absence or quantitative data). This property is of considerable importance since much of our knowledge concerning the distribution of organisms is based on presence-only information, which is not readily amenable for standard statistical models (Dettmers and Bart, 1999; Peterson et al., 2001). Additional advantages of CEMs are intuitive simplicity, clear theoretical basis (niche theory), applicability to different taxa, and straightforwardness of operation (Busby, 1991; Carpenter et al., 1993).

1.1. Limitations of CEMs

In spite of their wide use, CEMs have some noticed limitations. Three major limitations that have been recognized in previous studies are (1) inability to cope with correlations and interactions among the climatic factors, (2) assignment of equal suitability for all climatic combinations within the boundaries of the climatic envelope, and (3) sensitivity to outliers (Busby, 1991; Walker and Cocks, 1991; Carpenter et al., 1993; Shao and Halpin, 1995; Martin, 1996).

The first problem (i.e. disregarding possible interactions between climatic variables) stems from the rectilinear nature of the climatic envelope, that is, from the fact that the climatic niche of the species within the multidimensional space is bounded by straight lines/surfaces. This enveloping approach may overestimate the distribution boundaries of the modeled species if climatic variables are correlated (Skidmore et al., 1996). As an illustration, consider the climatic envelope in Fig. 1a. Due to the obvious correlation between the climatic variables, it seems reasonable to cast some combinations from the rectilinear envelope. Ignoring such correlation can result in overestimation of the distribution range.

The second limitation of CEMs is the fact that all climatic combinations within the boundaries of the climatic envelope are considered equally suitable for the modeled species (Shao and Halpin, 1995). Ecological theory, in contrast, asserts that species are distributed unequally along environmental gradients, with a tendency towards an

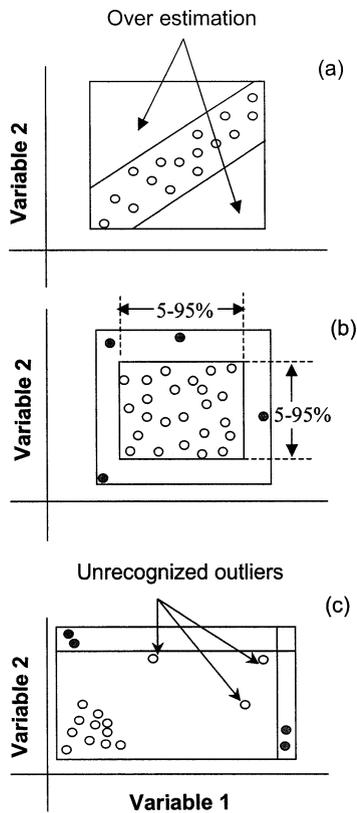


Fig. 1. Schematic illustrations of some limitations of rectilinear models. Circles represent the distribution of observations in a climatic space defined by two hypothetical variables. Gray circles are observations recognized as outliers. (a) In cases of correlations or interactions between climatic variables, the rectilinear model tends to overestimate the domain of climatic combinations represented by the data. (b) The boundaries of the climatic envelope are determined by the outermost data, and are therefore, sensitive to outliers. Using a certain percentile range (e.g. 5–95%) can reduce the impact of such outlying observations on model predictions. (c) Removal of outliers using the percentiles–range method may prove inadequate if observations are outliers in a multidimensional sense without being outliers (marginal) in any single dimension.

optimal value (Whittaker, 1975; Austin and Smith, 1989). Shao and Halpin (1995) proposed a modification of the enveloping algorithm that can be used to overcome this limitation. Specifically, instead of constructing a rectilinear envelope, they applied an enveloping algorithm that fits an elliptic envelope to the distributional data. Although the model proposed by Shao and Halpin

(1995) was based on various combinations of two climatic variables, their enveloping algorithm can be easily extended into a multidimensional climatic space. In this study we term the climatic envelope fitted by Shao and Halpin (1995) an upright elliptic envelope, since the axes of the ellipse used to define the climatic niche of the species are parallel to the climatic axes.

The third limitation of CEMs (sensitivity to outliers) originates from the fact that the boundaries of the climatic envelope are defined by the outermost observations (Fig. 1b). To reduce the impact of outlying observations on model predictions, users of CEMs often ‘chop’ the outermost values of each climatic variable by using only a certain percentile range of the data (Busby, 1991; Kershaw, 1997). For example, using the 5th–95th percentiles, 10% of the values for each climatic index (5% from each side) are automatically discarded, and only the remaining observations are used to construct the climatic envelope (Fig. 1b). Yet, while such a procedure may improve the performance of CEMs by reducing the probability of making false predictions of presence, it may also cause deterioration in predictive accuracy by increasing the rate of incorrect predictions of absences (Walker and Cocks, 1991; Eeley et al., 1999). In other words, there exists a tradeoff between errors of overestimation (commissions) and errors of underestimation (omissions). This tradeoff has rarely been analyzed in detail, and the literature provides examples for CEMs based on percentile ranges of 50% (Eeley et al., 1999), 80% (Law, 1994; Shao and Halpin, 1995), 90% (Nix, 1986; Sindel and Michael, 1992; Brereton et al., 1995), and 100% (i.e. the entire range, Podger et al., 1990; Richardson and McMahon, 1992; Sykes et al., 1996; Box et al., 1999).

It should also be noted that the standard procedure for outliers removal may prove inefficient in cases of observations that are relatively isolated along several climatic variables, but do not have extreme values on any particular variable (Fig. 1c). Although we would tend to classify such observations as outliers, they would not be excluded by the standard percentiles-range method.

1.2. A Mahalanobian approach for bioclimatic modeling

In this study we present an alternative approach for bioclimatic modeling, which allows for oblique positioning of an elliptic envelope within a multi-dimensional climatic space. The climatic envelope we propose is defined by climatic combinations having equal Mahalanobis distance (see below) to a vector of ‘optimal’ climatic conditions, with the ‘optimum’ being defined as the mean climatic conditions of all the observations available for the target species. An underlying assumption is that the modeled species is distributed optimally along niche axes, and that any deviation from the mean (optimal) conditions is associated with lower suitability. Such assumption is in accordance with niche theory, which suggests the existence of optimal environmental conditions for a species in

addition to maxima and minima, outside which the species cannot exist (Hutchinson, 1959; Whitaker, 1975). Thus, unlike the rectilinear approach, which relies on boundaries of distribution, the Mahalanobis distance technique relies on multi-variate mean and co-variance matrix. Fig. 2 summarizes the conceptual differences between the two modeling approaches.

Mathematically, the Mahalanobis distance between a vector x and a set S of vectors (matrix) is defined as:

$$D^2 = (x - m)^T C^{-1} (x - m)$$

where m is the mean vector and C is the covariance matrix of S (Clark et al., 1993). The ‘ T ’ superscript denotes the transpose operator. The rows (vectors) of S stand for observations and the columns for climatic indices. S , therefore, represents the climatic conditions of the sites where the species was recorded. The vector m represents the ‘optimum’ conditions, and x is a vector indicating climatic conditions of a particular site.

In general, the Mahalanobis distance is used to compute the distance between two centroids (Legendre and Legendre, 1998). Our application can, therefore, be considered as a special case where one centroid degenerates to a point. The correlations between climatic variables are reflected and compensated for by non-zero entries in off-diagonal portions of the covariance matrix (Clark et al., 1993). In cases of two or three dimensions, points with equal Mahalanobis distance lie on an ellipse or an ellipsoid, respectively. In general, equal Mahalanobis distances (D^2) imply equal similarities to the mean vector m (Seber, 1984).

When applied to species prediction, an underlying assumption of the Mahalanobis distance technique is that the mean vector represents optimal conditions for the species. Therefore, when the selection function is normally distributed, Mahalanobis distances are approximated by the χ^2 distribution with $n - 1$ degrees of freedom (n is the number of explanatory variables or the number of rows in S). Using this approximation, corresponding P -values can be assigned to potential sites (Clark et al., 1993). For many species, however, the assumption of normal distribution is

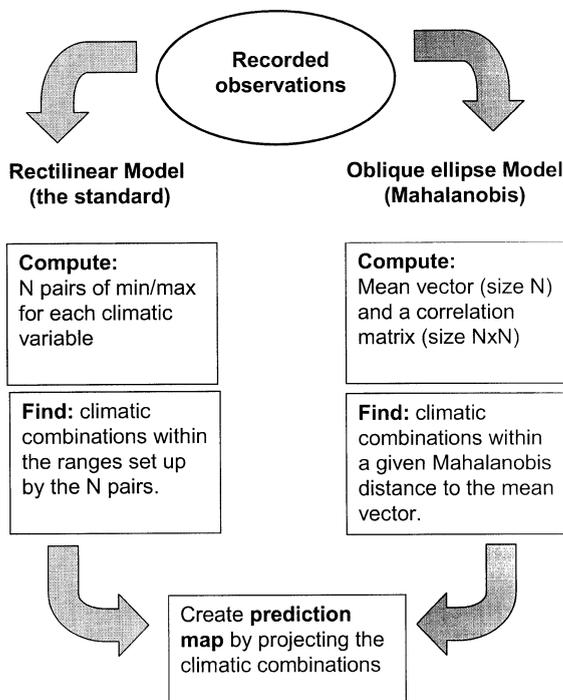


Fig. 2. Schematic chart of rectilinear vs. Mahalanobian models. Starting with a set of observations characterized by N climatic indices, both models define potential climatic envelopes in two steps (Compute and Find) and the climatic combinations constrained by these envelopes are projected to geographic space as predictive maps.

not satisfied (Austin and Smith, 1989). In such cases Mahalanobis distances can still be used to classify potential sites into quantiles (Knick and Dyer, 1997; Knick and Rotenberry, 1998) and the conversion to *P*-values serves merely to recode the Mahalanobis distances into a [0..1] scale (Clark et al., 1993).

1.3. Objectives of the study

This study was designed to test the hypothesis that CEMs applying the Mahalanobis distance as an enveloping algorithm, perform better (i.e. produce more accurate predictive maps) than models based on the rectilinear envelope. This hypothesis was based on the following rationales: (1) the climatic envelope generated by the Mahalanobis distance is oblique, and, therefore, may cope with correlations and interactions among the climatic variables; (2) the climatic envelope is elliptic, and, therefore, better reflects the principle of central tendency as expressed by niche theory; (3) model predictions are based on the whole data rather than on the outermost observations, and are, therefore, less sensitive to outliers.

We concentrated on woody plants as target species for our analysis. The floristic data we had (see Section 2) allowed us to use independent data for calibration and validation and to base our estimates of accuracy on high-quality reference data. This is an important advantage since data availability is a major obstacle for validating predictions of distribution models in general and CEMs in particular (Box et al., 1993; Fielding and Bell, 1997; Manel et al., 1999).

2. Methods

2.1. Climatic data

Three climatic factors were used to construct the CEMs in this study: mean annual rainfall, mean daily temperature of the hottest month (August), and average minimum temperature of the coldest month (January). These variables are known to have important effects on plant distribution (Woodward, 1987) and have been widely used in

previous applications of bioclimatic models (Busby, 1986; Richardson and McMahon, 1992; Skidmore et al., 1996; Box et al., 1999; Eeley et al., 1999). The sources of the rainfall and temperature data and the methodologies used to produce the climatic maps are described in previous papers (Kadmon and Heller, 1998; Kadmon and Danin, 1999; Kurtzman and Kadmon, 1999). For the purpose of this study, all climatic maps were standardized into a uniform spatial resolution of 1 km.

2.2. Floristic data

The floristic data used to develop the CEMs were compiled from the database of the Israel Nature and Parks Authority (INPA). This database consists of geo-referenced observations (spatial accuracy ± 100 m) collected by researchers, biologists and technical staff of the INPA in both protected and unprotected sites, over most regions of Israel. Further data were obtained from extensive phyto-sociological studies of the Negev Desert (Danin et al., 1975). Following McKenney et al. (1998), only species with more than 50 presence observations were selected for the analysis. The median number of observations per species in the final dataset was 159 and the overall dataset contained 129 species represented by 32414 observations that were distributed over 3606 sampling points covering the main climatic gradients of Israel (Fig. 3).

The validation tests were carried out using an independent database consisting of lists of species recorded by A. Danin for squares of 5×5 km covering about 95% of the study area. This grid database has already been used successfully to identify patterns of floristic variation in Israel (Danin and Plitmann, 1987; Kadmon and Danin, 1997, 1999). To maximize the reliability of the validation process, 96 squares (5×5 km each) were carefully selected from the overall grid database to fulfill three criteria: (1) maximal number of species recorded per square, (2) threshold distance between neighboring squares, and (3) uniform coverage of the study area. Criterion 1 assures that only well-sampled cells are used, and hence permits inference of absence if the species

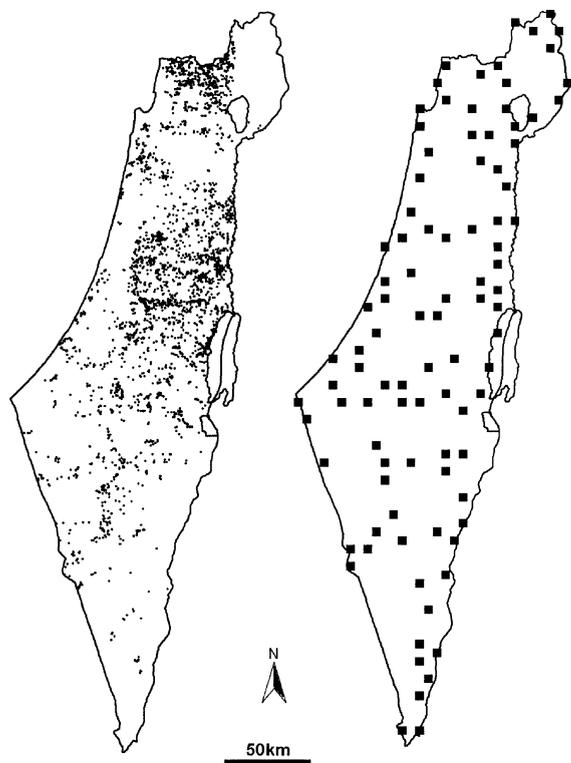


Fig. 3. Maps of the point observations used to develop the models (left) and the grid cells used for validation (right). The two maps are based on different databases. Note that the validation squares are spatially more uniform than the observations and better represent the overall study area.

has not been included in the list. Criterion 2 reduces the effect of spatial autocorrelation and criterion 3 guarantees that varieties of climatic combinations are represented. The geographical distribution of the selected validation squares is shown in Fig. 3.

2.3. Modeling procedure

For each of the 129 woody species, predictive maps were created using both the standard rectilinear approach and the Mahalanobian approach (Fig. 2). Considering previous studies indicating that predictions of rectilinear CEMs may depend on the percentile range used to remove outliers (Skidmore et al., 1996; Eeley et al., 1999), predictive maps of such models were constructed using percentile ranges of 100% (the min-max

range), 90, 80, 70, 60, and 50%. The basic procedure applied for constructing the rectilinear models consisted of five steps: (1) assembling the presence observations of the relevant species, (2) determining the climatic characteristics of each observation, (3) removing outliers by choosing a percentile range, (4) constructing a rectilinear climatic envelope based on the distribution of the remaining observations within the climatic space, and (5) projecting the climatic envelope back to the geographic space. The output of this process was raster maps (spatial resolution = 1 km^2) based on six different percentile ranges for each of the 129 species (a total of 774 maps).

Predictive maps based on the Mahalanobis distance were produced as follows. For a given species, the mean vector (m) and the correlation matrix (C) were first calculated from a matrix whose rows represent the sites where the species was recorded and the columns represent the corresponding values of the three climatic indices. Next, each $1 \times 1 \text{ km}^2$ grid cell in the study area was assigned with a Mahalanobis distance using m and C . Cells with Mahalanobis distance less than a predefined threshold (d) were considered as potentially suitable for the species and were included in the prediction. Since the rectilinear prediction is dichotomous (presence or absence) while the Mahalanobis prediction covers a continuous range of values, this procedure enabled us to compare the two methods. Note that the value of d is positively correlated with the area (volume) of the ellipse (ellipsoid). Hence, as d increases, so increases the chance that suitable climatic combinations would be included in the prediction. However, the chance to include superfluous combinations also increases. Based on a preliminary survey of this tradeoff, d was set to 4 in all models. Under the assumption of normality, this threshold corresponds to a probability of 0.86.

The manner by which the two types of predictive maps were created is demonstrated in Figs. 4 and 5 using the plant *Phlomis brachyodon* (an Irano-Turanian semi-shrub) as an example. First, the geographic observations of the species were mapped within the climatic space (Fig. 4). Within this space, two enveloping approaches were applied: rectilinear and Mahalanobian. Next, the

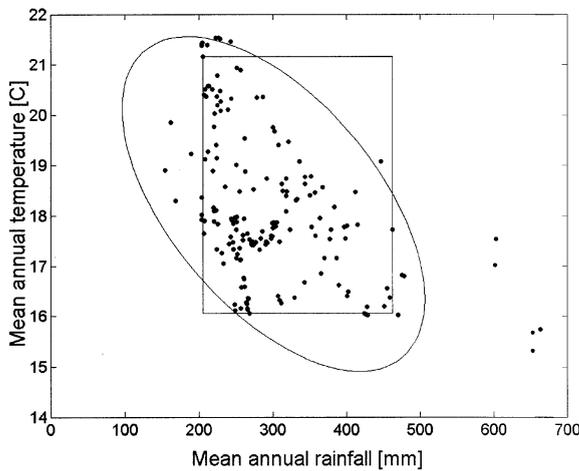


Fig. 4. Mahalanobis vs. rectilinear envelopes produced for the semi-shrub *P. brachyodon*. The points represent observations of *P. brachyodon* in a climatic space defined by two variables: mean annual rainfall and mean annual temperature. The rectilinear envelope was produced using the standard (BIOCLIM) approach with a percentile range of 90%. The elliptic envelope was generated using the Mahalanobis distance technique.

climatic combinations of each envelope were projected back into the geographical space to form two maps of potential distribution, each representing a different modeling approach (Fig. 5). Note that, for visualization purposes, the climatic space presented in Fig. 4 is limited to two dimensions. The resultant maps however, (Fig. 5), as all predictive maps in this study, were constructed using three climatic indices (mean annual rainfall, minimal temperature of January and mean temperature of August).

2.4. Validation procedure

All predictive maps were created at a spatial resolution of 1 km^2 , which was the resolution of the climatic maps. In order to make the predictive maps spatially compatible with the validation squares, they were downscaled to a grid of $5 \times 5 \text{ km}$. A grid cell of 25 km^2 was marked as 'predicted presence' for a given species if the species was predicted to occur in at least one of the 1 km^2 cells that are bounded by it. Otherwise, the square was considered as 'predicted absence'.



Mahalanobis Observations Rectilinear

Fig. 5. Predictive maps produced for the semi-shrub *P. brachyodon*. The map on the left shows the prediction of the Mahalanobian model. Darker tones indicate higher potential suitability, i.e. greater similarity to the mean climatic conditions. The map on the right shows the prediction of a rectilinear model based on a percentile range of 90%. Both predictions were generated using the same observations (middle). Crosses indicate known presences of *P. brachyodon* based on the validation database. Note that for this species, the rectilinear model tends to exaggerate the potential distribution of the species.

Each predictive map was checked at the 96 validation squares and the results were summarized in an error matrix (Table 1) from which four measures of accuracy were calculated: sensitivity, specificity, overall accuracy, and the Kappa statistic (Table 2; Fielding and Bell, 1997; Legendre and Legendre, 1998). Sensitivity is defined as the probability of correctly predicting a presence, whereas specificity is the probability of correctly predicting an absence (Fielding and Bell, 1997). The advantage of sensitivity and specificity is that they are not dependent on the prevalence of the species. This, however, is not the case with overall accuracy, which tends to ascribe high accuracies for rare species (Fielding and Bell, 1997; Manel et al., 1999). The Kappa statistic (Cohen, 1960) compensates for this bias by evaluating the accuracy of prediction relative to the accuracy that might have resulted by chance alone (Monserud and Leemans, 1992).

Table 1
An error matrix used to evaluate the accuracy of model predictions

		Validation dataset	
		Presence	Absence
Model	Presence	a	b
	Absence	c	d

Component	Interpretation
a	Number of cells for which presence was correctly predicted by the model.
b	Number of cells for which the species was not found but the model predicted presence.
c	Number of cells for which the species was found but the model predicted absence.
d	Number of cells for which absence was correctly predicted by the model.

The components *a*, *b*, *c* and *d*, stand for frequencies of cases representing the four possible outcomes of a comparison between a predictive map and a validation dataset.

2.5. Software tools

ESRI ARCVIEW (ESRI, 1998) was used for GIS analyses and map production. MathWorks MATLAB (MathWorks, 1999) was used for numerical simulations, mathematical analyses and graph production. Standard statistical analyses were performed using SPSS (SPSS, 1999).

3. Results

Fig. 6 compares the performance of the two modeling approaches by showing the median

values ($n = 192$ species) obtained for the four measures of accuracy (overall accuracy, Kappa, specificity and sensitivity). The values obtained for the rectilinear model are shown as functions of the percentile range, whereas those obtained for the Mahalanobian model are represented by a dashed reference line. As expected, predictive accuracy of the rectilinear model was sensitive to the percentile range used to select the observations. Yet, for all percentile ranges, the Mahalanobian model revealed higher values of both overall accuracy and Kappa, than the rectilinear one (Fig. 6a, b). Similar patterns were obtained using the mean values of the two measures (not shown).

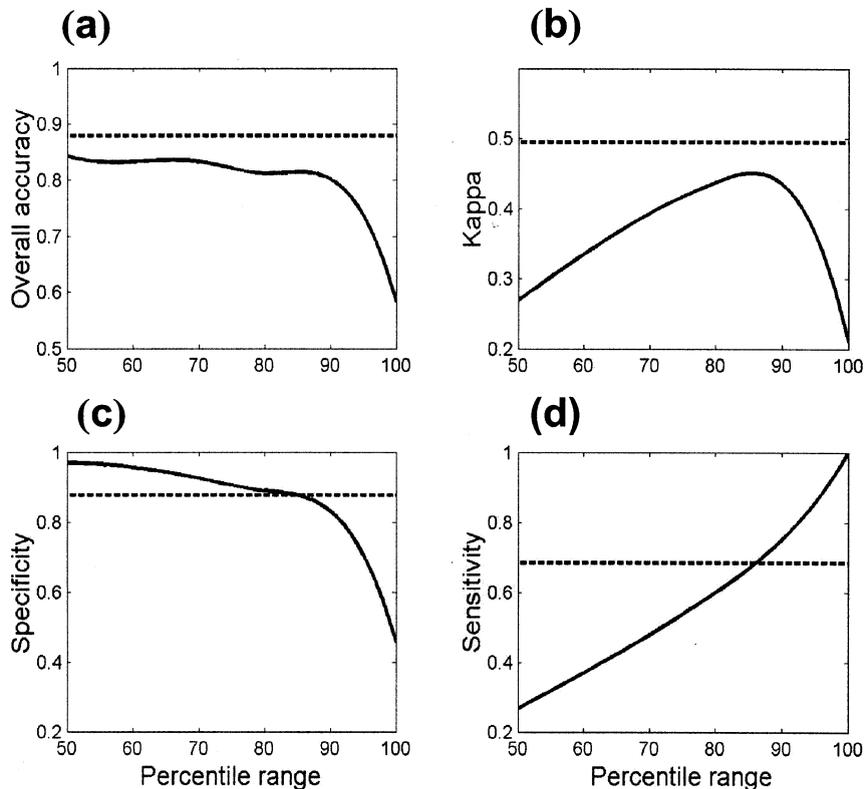


Fig. 6. Accuracy assessment of predictive maps produced by rectilinear (solid lines) vs. Mahalanobis (dashed lines) models. Four measures of accuracy are shown as ordinates: Overall accuracy (a), Kappa (b), Specificity (c), and Sensitivity (d). The plots show median values of the four measures, based on predictive maps produced for 129 species. In all plots, the abscissa represents the percentile range used to construct the rectilinear envelope.

Examination of the results obtained for specificity (the probability to correctly predict an absence) and sensitivity (the probability to correctly predict a presence) helps to understand these results. In the case of the rectilinear model, specificity was a decreasing function of the percentile range, and crossed the line representing the Mahalanobian model at a percentile range of about 85% (Fig. 6c). The values obtained for sensitivity exhibited an opposite trend, i.e. a monotonically increasing function that crossed the Mahalanobian curve at a percentile range of about 85% (Fig. 6d). Below the crossing point, the gain in sensitivity achieved by the Mahalanobian model was higher than the corresponding decrease in specificity (compare Fig. 6c, d). Above the crossing point, the decrease in sensitivity was lower than the gain in specificity. As a consequence,

values of overall accuracy and Kappa obtained for the Mahalanobian model were higher than those obtained for the rectilinear model over the whole spectrum of percentile ranges.

Using the median (or mean) values may blur the results of the analysis due to high among-species variability in the various measures of accuracy. Therefore, the two modeling approaches were further compared on a per-species basis, by calculating the difference in accuracy between the Mahalanobian and rectilinear models. For this comparison, the 'best' percentile range (5th–95th) was chosen to represent the rectilinear model. The results are shown in Fig. 7. The bar corresponding to zero in all histograms represents the number of species for which equal or nearly equal accuracy was obtained for both models. Bars left to zero show the number of species for which the recti-

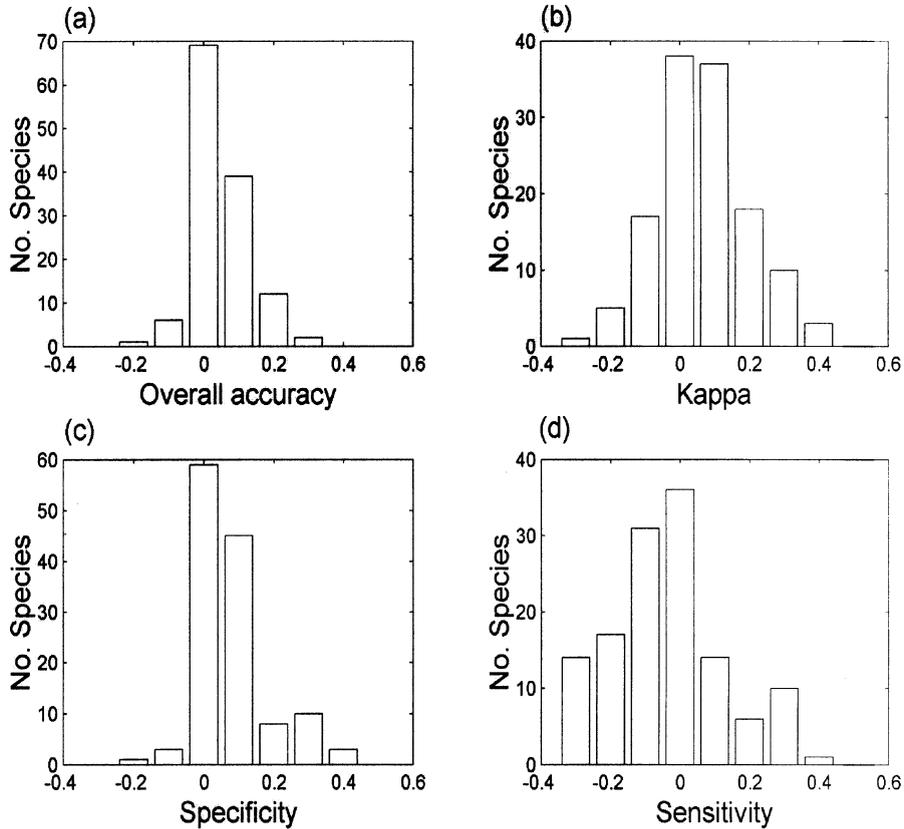


Fig. 7. Species-level comparisons between the Mahalanobis and rectilinear models. For each species, the four measures of accuracy (Overall accuracy, Kappa, Specificity and Sensitivity) were calculated based on prediction maps of the two models. The abscissa represents the difference between the accuracy of the Mahalanobis model and that of the rectilinear model. The ordinate is the number of species in each difference category.

linear model was more accurate, whereas bars to the right indicate cases for which the Mahalanobian model was more accurate. The distance of a bar from zero represents the magnitude of the difference in accuracy between the two modeling approaches.

Examination of the histograms indicates that the Mahalanobian model was superior in many cases, but equal, or even inferior to the rectilinear model in other cases. For example, 37 species (~29%) showed an improvement of about 0.1 in Kappa when modeled by the Mahalanobian model, but 17 species (~13%) showed a deterioration of similar rate (Fig. 7b). Yet, a paired *t*-test based on the values of Kappa obtained for the 129

species verified that the Mahalanobian model was significantly more accurate ($P < 0.001$) than the rectilinear one.

Further insights for these results were obtained by comparing the histograms of specificity and sensitivity (Figs. 7c and 7d). For 66 species, the sensitivity of prediction was higher with the rectilinear model, and for 34 the sensitivity was equal or nearly equal. However, for 105 species, specificity was higher with the Mahalanobian model. Thus, the disadvantage of the Mahalanobian model in terms of sensitivity was more than compensated by its gain in specificity.

To supplement the above analyses, McNemar's test (Huberty, 1994; Fielding and Bell, 1997) was

Table 2
Measures of predictive accuracy calculated from a 2×2 error matrix (Table 1)

Measure	Formula
Overall accuracy	$\frac{a + d}{n}$
Kappa statistic	$\frac{\left(\frac{a + d}{n}\right) - \frac{(a + b)(a + c) + (c + d)(d + b)}{n^2}}{1 - \frac{(a + b)(a + c) + (c + d)(d + b)}{n^2}}$
Sensitivity	$\frac{a}{a + c}$
Specificity	$\frac{d}{b + d}$

Overall accuracy is the rate of correctly classified cells. The Kappa statistic normalizes the overall accuracy by the accuracy that might have occurred by chance alone. Sensitivity is the probability that the model will correctly classify a presence, and Specificity is the probability that the model will correctly classify an absence. In all formulas $n = a + b + c + d$.

applied for each species separately to examine which model prediction was more accurate in relation to the validation set. For two species, the predictions of the rectilinear model were significantly more accurate (at $\alpha = 0.05$), whereas for 36 species the Mahalanobian model was significantly more accurate. Non-significant results were obtained for the remaining 91 species.

4. Discussion

4.1. Concepts and limitations

The prediction of a CEM, termed climatic potential niche, should not to be confused with the climatic fundamental niche, which comprises the climatic combinations that the species can tolerate within a multidimensional space (Whittaker, 1975; Guisan et al., 1999). Frequently, the potential niche is a subset of the fundamental niche because the observations upon which the CEMs are constructed do not cover the entire

climatic range of the species. This may happen either because the species was not sampled under certain climatic combinations within the study area, or because its distribution extends beyond the study area.

The climatic potential niche should neither be confused with the realized niche (Hutchinson, 1959; Austin, 1999), which is usually smaller due to the effect of dispersal limitations, competition, edaphic factors, microhabitat conditions, anthropogenic disturbances etc. Conceptually, the climatic potential niche can be viewed as an interpolation of the presence data, lying ‘some-where’ between the realized and fundamental niches.

The distinction between the fundamental, potential, and realized niches is important for the interpretation of the validation tests. Obviously, predictive maps can only be validated through comparison with maps of actual distribution. In the case of CEM predictions, this validation procedure assumes that climate is a dominant factor in determining species distribution. Under this assumption, we treat the potential niche as an approximation to the realized niche, and use the later to validate the former. Although this assumption is reasonable for relatively large spatial scales (Box et al., 1993; Huntley et al., 1995), it nevertheless becomes problematic for local scales in which non-climatic factors are likely to have crucial impact on species distribution (Pulliam, 2000).

Two other factors that may have influenced the results of our analyses are the number (and identity) of climatic variables used to construct the CEMs, and the threshold number of 50 observations used to select species for the analyses. Since the main aim of our analysis was to compare (and interpret) predictive maps generated by different modeling approaches, we based our models on a limited number of climatic variables that have previously been recognized as important determinants of plant distribution patterns. Yet, since previous applications of CEMs were usually based on larger sets of climatic indices, it might be argued that our results are not applicable to CEMs in general. To evaluate this argument we ran additional simulations in which we varied the

number and identity of variables used to construct the climatic envelopes. The results obtained from these simulations (not shown) were in agreement with those obtained for the original models. For example, doubling the number of variables used to construct the rectilinear models resulted in a 6% increase in average predictive accuracy. This result is consistent with Peterson and Cohoon (1999) who found convergence of model performance with 4–5 climatic variables, and can be attributed to the existence of high correlations between the climatic factors.

Further simulations were performed to evaluate whether the threshold number of 50 observations per species was sufficient to obtain reasonable predictions. These simulations were based on 54 species having more than 200 observations. For each species, a trial number of observations, n , was determined ($n = 10, 20, 50, 75, 100, 150$ and 200), and 150 random sets (repetitions) of n observations were selected, each time creating a predictive map based upon the selected observations. This process generated 56 700 maps ($54 \text{ species} \times 7 \text{ sample sizes} \times 150 \text{ repetitions}$). The accuracy of each map was determined using the validation dataset, and the mean value of Kappa was calculated for each sample size (n). The results indicated that 50 observations were sufficient to approximate the asymptotic value of Kappa. Doubling the number of observations from 50 to 100 led to a corresponding increase of 2.4% in predictive accuracy, while further increase in the number of observations did not improve the accuracy of model predictions. These results justify the threshold number of observations used to select the species for our analysis.

4.2. Rectilinear versus Mahalanobian modeling

In theory, the ability to incorporate climatic correlations into the modeling algorithm is a major advantage of the Mahalanobian model over the rectilinear one. We use the term Correlation here to indicate a mathematical relation (positive or negative) between climatic indices of the sites where a species was recorded. Such correlation does not necessarily imply interaction, which is the mutual effect of two (or more) factors in determin-

ing the likelihood of a species' occurrence at a site. For example, due to historical reasons, the distribution range of a species can be confined to an area in which rainfall and temperature are strongly correlated, but clearly this correlation does not signify interaction. Genuine interaction may occur, for example, when lower rainfall is compensated for by lower evaporation at a site with lower temperatures (Nix, 1986; Busby, 1991; Huntley et al., 1995). In cases where the observed correlation does not reflect genuine interaction, the Mahalanobian model is likely to produce inadequate climatic envelopes, with a possible distortion of the species' climatic requirements. This problem is of particular significance in cases where predictions of CEMs are extrapolated into areas where climatic correlations are different from those characterizing the area where the model was developed.

Linear CEMs are known to overestimate species distribution (Walker and Cocks, 1991; Skidmore et al., 1996). However, it is important to distinguish between two types of overestimation. The first occurs when a climatically suitable area is restricted from the species due to non-climatic factors. For example, competition or limited dis-

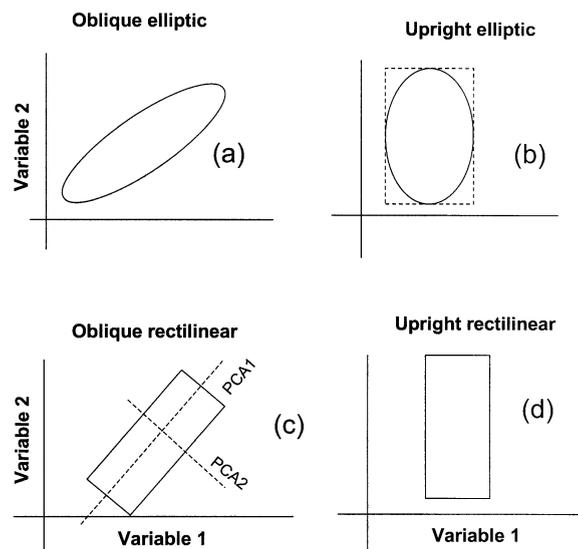


Fig. 8. Schematic representation of the four modeling approaches compared in Table 3.

persal ability may prevent a species from utilizing its fundamental niche (Pulliam, 2000). The second overestimation may result when inappropriate climatic combinations (viz. beyond the climatic tolerance of the species) are included in the prediction. Such overestimation, unlike the former, indicates a ‘true’ modeling error. The first type of overestimation can be corrected by incorporating additional environmental variables into the analysis (Austin et al., 1990; Eeley et al., 1999; Wright et al., 2000). The second overestimation can be rectified by producing ‘tighter’ climatic envelopes in which extraneous climatic combinations are excluded from the prediction. In rectilinear CEMs, this is done by removing outlying observations from the dataset before the climatic envelope is determined. The Mahalanobian model rectifies such overestimation by using an algorithm that fits an ellipsoid, rather than a rectilinear hyperspace, to the climatic data (Fig. 4). In this study, removal of outliers improved the accuracy of rectilinear models, but nevertheless, the Mahalanobian models produced significantly more accurate predictions (Fig. 6).

4.3. Interpretation of the results

This study was motivated by the assumption that Mahalanobian modeling has three principal advantages over rectilinear modeling: the ability to cope with climatic correlations, the ability to take into account central tendency in species responses to climatic gradients, and the ability to take into account the climatic characteristics of all observa-

tions in determining the boundaries of the climatic envelope. Our results support the hypothesis that Mahalanobian models are superior to rectilinear ones, but they do not prove that this superiority a consequence of these underlying theoretical advantages.

To examine this question, we developed two additional types of models. The first model was based on an elliptic envelope without a tilt (Fig. 8b). This envelope was enclosed within the rectilinear envelope. The straightforward formulation of this upright elliptic envelope can be found in Shao and Halpin (1995). The second model was based on an oblique rectilinear envelope (Fig. 8c). To construct this envelope, principal components analysis (PCA) was used to establish a new 3D coordination system whose tilt represents the correlation between the climatic indices. In both models (as in the ordinary rectilinear model), the 5th–95th percentiles range was used to cast outlying values.

If the ability to cope with climatic correlations was the underlying reason for the superiority of the Mahalanobian model, one would expect that the oblique rectilinear model (Fig. 8c) would be as accurate as the Mahalanobian model. Alternatively, if the improvement in accuracy was due to the elliptic shape, which emphasizes central tendency, than the upright elliptic model (Fig. 8b) should be as accurate as the Mahalanobian model. If both mechanisms contributed to the superiority of the Mahalanobian model, predictions based on both the upright elliptic envelope and the oblique rectilinear envelope should be more accurate than

Table 3
Accuracy assessment of predictive maps produced for 129 species of woody plants

Measure of accuracy	Modeling approach			
	Oblique elliptic (Mahalanobian)	Upright elliptic	Oblique rectilinear	Upright rectilinear
Overall accuracy	0.82	0.77	0.79	0.78
Kappa	0.48	0.39	0.37	0.41
Specificity	0.86	0.78	0.86	0.78
Sensitivity	0.70	0.73	0.55	0.74

The distribution of each species was predicted using four different modeling approaches (see Fig. 8 for details). The performance of each modeling approach is expressed by the mean values of four measures of accuracy (overall accuracy, Kappa, specificity and sensitivity).

those based on the standard (upright) rectilinear model. But if the superiority of the Mahalanobian model is related to the fact that it uses all the available data, then neither the upright elliptic envelope, nor the oblique rectilinear envelope should enhance predictive accuracy relative to the standard rectilinear model.

To distinguish between these alternatives, we applied an upright elliptic model (Fig. 8b) and an oblique rectilinear model (Fig. 8c) for each of the 129 species. Table 3 compares the accuracy of predictions generated by these models with the results obtained for the standard (rectilinear) model and the Mahalanobian model. Surprisingly, the performance of the two new models (expressed by overall accuracy and Kappa) was significantly lower than that of the Mahalanobian model. Furthermore, in terms of Kappa (which is the most informative measure of accuracy), the performance of the new models was lower even in relation to the rectilinear model! Further simulations (not shown) revealed that models based on oblique ellipses (i.e. applying Shao and Halpin (1995) technique to the PCA-transformed data) were still less accurate than Mahalanobian models, albeit the shape of the climatic envelope was similar.

These findings suggest (but not prove) that the superiority of the Mahalanobian model originated from its ability to consider the entire distributions of the climatic indices. The boundaries of non-Mahalanobian envelopes (Fig. 8b–d) are determined by the percentile range, that is, by the outermost values of the climatic indices. In contrast, the Mahalanobian envelope (Fig. 8a) determines the suitability of a climatic combination according to its dissimilarity with the ‘optimal’ climatic vector whose value is determined by all the observations. We conclude that this difference was the main reason for the observed superiority of the Mahalanobian model.

Acknowledgements

We thank A. Danin and the INPA for providing us the floristic data. We also thank Adi Ben-Nun for continuous assistance with GIS issues. The

study was supported by the GIS Center of the Hebrew University. Financial support for the study was provided by the Rieger Foundation, the Ring Foundation, and the Nature and Parks Authority.

References

- Austin, M.P., 1999. A silent clash of paradigms: some inconsistencies in community ecology. *Oikos* 86, 170–178.
- Austin, M.P., Smith, A.P., 1989. A new model for continuum concept. *Vegetatio* 83, 35–47.
- Austin, M.P., Nicholls, A.O., Margules, C.R., 1990. Measurement of the realized qualitative niche-environmental niches of 5 eucalyptus species. *Ecological Monographs* 60, 161–177.
- Bolliger, J., Kienast, F., Bugmann, H., 2000. Comparing models for tree distributions: concept, structures, and behavior. *Ecological Modelling* 134, 89–102.
- Booth, T.H., Nix, H.A., Hutchinson, M.F., Jovanovic, T., 1988. Niche analysis and tree species introduction. *Forest Ecology and Management* 23, 47–59.
- Box, E.O., Crumpacker, D.W., Hardin, E.D., 1993. A climatic model for location of plant species in Florida, USA. *Journal of Biogeography* 20, 629–644.
- Box, E.O., Crumpacker, D.W., Hardin, E.D., 1999. Predicted effects of climatic change on distribution of ecologically important native tree and shrub species in Florida. *Climatic Change* 41, 213–248.
- Brereton, R., Bennet, S., Mansergh, I., 1995. Enhanced greenhouse climate change and its potential effect on selected fauna of south-eastern Australia: a trend analysis. *Biological Conservation* 72, 339–354.
- Busby, J.R., 1986. A biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in southeastern Australia. *Australian Journal of Ecology* 11, 1–7.
- Busby, J.R., 1991. BIOCLIM—a bioclimatic analysis and prediction system. In: Margules, C.R., Austin, M.P. (Eds.), *Nature Conservation*. CSIRO, Australia, pp. 64–68.
- Carpenter, G., Gillison, A.N., Winter, J., 1993. DOMAIN—a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation* 2, 667–680.
- Clark, J.D., Dunn, J.E., Smith, K.G., 1993. A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management* 57, 519–526.
- Cohen, J., 1960. A coefficient of agreement of nominal scales. *Educational and Psychological Measurement*, 20, 37–46.
- Danin, A., Orshan, G., Zohary, M., 1975. The vegetation of the Northern Negev and the Judean Desert of Israel. *Israel Journal of Botany* 24, 118–172.

- Danin, A., Plitmann, U., 1987. Revision of the plant geographical territories of Israel and Sinai. *Plant Systematics and Evolution* 150, 43–53.
- Dettmers, R., Bart, J., 1999. A GIS modelling method applied to predicting forest songbird habitat. *Ecological Applications* 9, 152–163.
- Eeley, H.A.C., Lawes, M.J., Piper, S.E., 1999. The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. *Journal of Biogeography* 26, 595–617.
- ESRI ARCVIEW, Version 3.1. ESRI, Redlands, CA 1998.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24, 38–49.
- Franklin, J., 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* 19, 474–499.
- Godoun, M., Peterson, A.T., 2000. Preliminary distributional analysis of US endangered bird species. *Biodiversity and Conservation* 9, 1313–1322.
- Guisan, A., Weiss, S.B., Weiss, A.D., 1999. GLM versus CCA spatial modelling of plant species distribution. *Plant Ecology* 143, 107–122.
- Honig, M.A., Cowling, R.M., Richardson, D.M., 1992. The invasive potential of Australian banksias in South African fynbos: a comparison of the reproductive potential of *Banksia ericifolia* and *Leucadendron laurolum*. *Australian Journal of Ecology* 17, 305–314.
- Huberty, C.J., 1994. *Applied Discriminant Analysis*. Wiley-Interscience, New York, USA.
- Huntley, B., Berry, P.M., Cramer, W., McDonald, A.P., 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography* 22, 967–1001.
- Hutchinson, G.E., 1959. Homage to Santa Rosalia, or why are there so many kinds of animals. *American Naturalist* 93, 145–159.
- Hutchinson, M.F., 1995. Interpolating mean rainfall using thin plate smoothing splines. *International Journal of Geographical Information Systems* 9, 385–403.
- Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs* 68, 465–485.
- Kadmon, R., Danin, A., 1997. Floristic variation in Israel: a GIS analysis. *Flora* 192, 341–345.
- Kadmon, R., Heller, J., 1998. Modelling faunal responses to climatic gradients with GIS: land snails as a case study. *Journal of Biogeography* 25, 527–539.
- Kadmon, R., Danin, A., 1999. Distribution of plant species in Israel in relation to spatial variation in rainfall. *Journal of Vegetation Science* 10, 421–432.
- Karl, J.W., Heglund, P.J., Garton, E.O., Scott, J.M., Wright, N.M., Hutto, R.L., 2000. Sensitivity of species habitat-relationship model performance to factors of scale. *Ecological Applications* 10, 1690–1705.
- Kershaw, A.P., 1997. A bioclimatic analysis of early to Middle Miocene brown coal floras, Latrobe Valley, south-eastern Australia. *Australian Journal of Botany* 45, 373–387.
- Knick, S.T., Dyer, D.L., 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management* 61, 75–85.
- Knick, S.T., Rotenberry, J.T., 1998. Limitations to mapping habitat use areas in changing landscapes using the Mahalanobis distance. *Journal of Agricultural, Biological and Environmental Statistics* 3, 311–322.
- Kurtzman, D., Kadmon, R., 1999. Mapping of temperature variables in Israel: a comparison of different interpolation methods. *Climate Research* 13, 33–43.
- Law, B.S., 1994. Climatic limitation of the southern distribution of the common blossom bat *Syconycteris australis* in New South Wales. *Australian Journal of Ecology* 19, 366–374.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*, second edn. Elsevier, Amsterdam.
- Lindenmayer, D.B., Nix, H.A., McMahon, J.P., Hutchinson, M.F., Tanton, M.T., 1991. The conservation of leadbeaters's possum, *Gymnobelideus leadbeateri* (McCoy): a case study of the use of bioclimatic modelling. *Journal of Biogeography* 18, 371–383.
- Manel, S., Dias, J.M., Ormerod, S.J., 1999. Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. *Ecological Modelling* 120, 337–347.
- Martin, W.K., 1996. The current and potential distribution of the common myna *Acridotheres tristis* in Australia. *Emu* 96, 166–173.
- MathWorks MATLAB, Version 5.3. The Mathworks, Natick, MA 1999.
- McKenney, D.W., Mackey, B.G., Bogart, J.P., McKee, J.E., Oldham, M.J., Chek, A., 1998. Bioclimatic and spatial analysis of Ontario reptiles and amphibians. *Ecoscience* 5, 18–30.
- McKenzie, G.M., Busby, J.R., 1992. A quantitative estimate of Holocene climate using a bioclimatic profile of *Nothofagus-cunninghamii* (hook) Oerst. *Journal of Biogeography* 19, 531–540.
- Monserud, R.A., Leemans, R., 1992. Comparing global vegetation maps with the Kappa-statistic. *Ecological Modelling* 62, 275–293.
- Monserud, R.A., Tchepakova, N.M., Denissenko, O.V., 1998. Reconstruction of the mid-Holocene palaeoclimate of Siberia using a bioclimatic vegetation model. *Palaeogeography Palaeoclimatology Palaeoecology* 139, 15–36.
- Nix, H.A., 1986. A biogeographic analysis of Australian elapid snakes. In: *Atlas of Elapid Snakes of Australia*. Australian Government Publications Service, Canberra, pp. 4–15.
- Pearce, J., Lindenmayer, D., 1998. Bioclimatic analysis to enhance reintroduction biology of the endangered helmeted honeyeater (*Lichenostomus melanops cassidix*) in south-eastern Australia. *Restoration Ecology* 6, 238–243.

- Pearce, J., Ferrier, S., 2001. The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation* 98, 33–43.
- Peterson, A.T., Cohoon, K.P., 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecological Modelling* 117, 159–164.
- Peterson, A.T., Stockwell, D.R.B., Kluza, D.A., 2001. Distributional prediction based on ecological niche modelling of primary occurrence data. In: Scott, J.M., Heglund, P.J., Morrison, M., Raphael, M., Hauffler, J., Wall, B., Samson, F. (Eds.), *Predicting Species Occurrences: Issues of Scale and Accuracy*. Island Press, Covello, CA.
- Podger, F.D., Mummery, D.C., Palzer, C.R., Brown, M.J., 1990. Bioclimatic analysis of the distribution of damage to native plants in Tasmania by *Phytophthora cinnamomi*. *Australian Journal of Ecology* 15, 281–290.
- Pulliam, H.R., 2000. On the relationship between niche and distribution. *Ecology Letters* 3, 349–361.
- Richardson, D.M., McMahon, J.P., 1992. A bioclimatic analysis of *Eucalyptus-nitens* to identify potential planting regions in Southern Africa. *South Africa Journal of Science* 88, 380–387.
- Seber, G.A.F., 1984. *Multivariate Observations*. Wiley, USA.
- Shao, G.F., Halpin, P.N., 1995. Climatic controls of eastern north American coastal tree and shrub distributions. *Journal of Biogeography* 22, 1083–1089.
- Sindel, B.M., Michael, P.W., 1992. Spread and potential distribution of *Senecio madagascariensis* Poir. (fire weed) in Australia. *Australian Journal of Ecology*, 17, 21–26.
- Skidmore, A.K., Gauld, A., Walker, P.A., 1996. Classification of kangaroo habitat distribution using three GIS models. *International Journal of Geographical Information Systems* 10, 441–454.
- SPSS for WINDOWS, Rel. 10.0.0. SPSS, Chicago, IL 1999.
- Stockwell, D., Peters, D., 1999. The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science* 13, 143–158.
- Sykes, M.T., Prentice, I.C., Cramer, W., 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography* 23, 203–233.
- Walker, P.A., Cocks, K.D., 1991. HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography Letters* 1, 108–118.
- Whittaker, R.H., 1975. *Communities and Ecosystems*, second ed.. Macmillan, New York.
- Woodward, I., 1987. *Climate and Plant Distribution*. Cambridge University Press, Cambridge.
- Wright, A., Fielding, A.H., Wheeler, C.P., 2000. Predicting the distribution of Eurasian badger (*Meles meles*) setts over an urbanized landscape: a GIS approach. *Photogrammetric Engineering and Remote Sensing* 66, 423–428.