

Usefulness of Bioclimatic Models for Studying Climate Change and Invasive Species

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Bioclimatic models (also known as envelope models or, more broadly, ecological niche models or species distribution models) are used to predict geographic ranges of organisms as a function of climate. They are widely used to forecast range shifts of organisms due to climate change, predict the eventual ranges of invasive species, infer paleoclimate from data on species occurrences, and so forth. Several statistical techniques (including general linear models, general additive models, climate envelope models, classification and regression trees, and genetic algorithms) have been used in bioclimatic modeling. Recently developed techniques tend to perform better than older techniques, although it is unlikely that any single statistical approach will be optimal for all applications and species. Proponents of bioclimatic models have stressed their apparent predictive power, whereas opponents have identified the following unreasonable model assumptions: biotic interactions are unimportant in determining geographic ranges or are constant over space and time; the genetic and phenotypic composition of species is constant over space and time; and species are unlimited in their dispersal. In spite of these problematic assumptions, bioclimatic models often successfully fit present-day ranges of species. Their ability to forecast the effects of climate change or the spread of invaders has rarely been tested adequately, however, and we urge researchers to tie the evaluation of bioclimatic models more closely to their intended uses.

Key words: alien species; AUC; bioclimatic models; climate change; Cohen's kappa; diseases; ecological niche models; envelope models; exotic species; GARP; geographic ranges; independent validation; introduced species; invasive species; naturalized species; nonindigenous species; non-native species; paleoecology; species distribution models

Introduction

The understanding of species' geographic ranges (the areas where these species occur) is an important and classical ecological challenge (Brown *et al.* 1996; Gaston 2003). It has been on researchers' agendas for a long time and has recently received additional attention as a result of global change and the correspond-

ing need to predict range shifts due to climate change, to estimate where an invasive species or disease will spread, or to predict the fate of endangered species. Another reason for the renewed interest in geographic ranges is the rise of macroecology, which studies "relationships between organisms and their environment that involve characterizing and explaining statistical patterns of abundance, distribution, and diversity" (Brown 1995, p. 10; see also Brown & Maurer 1989; Blackburn & Gaston 2003).

Particularly important tools in studies of the geographic range are bioclimatic models, also known as envelope models (Kadmon *et al.*

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2003), climate response surfaces (Huntley 1995), homoclines (Weber 2001), or—more broadly—ecological niche models (Peterson & Vieglaiss 2001) or species distribution models (Loiselle *et al.* 2003). These models have become very popular in recent years. In this review, we outline the general approach of bioclimatic modeling, discuss objections that have been made to this approach, review different statistical methods used in bioclimatic modeling, list current applications, evaluate the general contributions of bioclimatic modeling, and indicate present obstacles and needs, thereby suggesting future directions.

Despite their wide use, bioclimatic models are controversial. Their proponents have praised the models' apparent predictive power: "Species that have been examined are diverse, including plants and animals, freshwater and terrestrial species, and vertebrates and invertebrates. Almost invariably, predictivity [...] has been excellent" (Peterson 2003, p. 426). On the other hand, opponents have pointed out unreasonable model assumptions: "Climate envelope approaches might be inadequate for many species" (Sax *et al.* 2007, p. 468). We will show that neither extreme viewpoint is supported by currently available information.

How Is It Done? Bioclimatic Modeling Approaches

General Approach

The idea that geographic ranges of species are determined by climatic conditions was mentioned as early as the beginning of the 19th century (Latreille 1819, cited by Davis *et al.* 1998a). This idea forms the basis of bioclimatic models, which can be grouped into two classes. The first consists of mechanistic models, which use a species' physiological tolerance to factors, such as heat, cold, or frost, to predict this species' range (Doley 1977; Patterson *et al.* 1979; Prentice *et al.* 1992; Sykes *et al.* 1996; Kearney & Porter 2004; Hijmans & Graham 2006). The physiological tolerances are usually measured in the laboratory, then applied to

field conditions. By contrast, empirical models, which form the other and larger class of bioclimatic models, apply a top-down approach. Here, physiological tolerances are unknown or disregarded in the modeling process. It is not even assumed that a species' geographic range is directly determined by physiological tolerance. Instead, a number of climatic variables (e.g., temperature [minimum, maximum, average], precipitation, evapotranspiration) are measured for many different locations, often cells in a grid, and statistically compared to the occurrence of the focal species at these locations. This procedure yields the climatic range limits of this species' distribution and allows the prediction of, for example, range shifts due to climate change. In some models, nonclimatic variables of potential importance (e.g., edaphic or land-use variables) are included as well. A wide range of statistical models have been used, which will be discussed later in this paper.

Key Assumptions

Like all models, bioclimatic models make a number of assumptions that are not strictly met in nature (Box 1; Woodward & Beerling 1997; Davis *et al.* 1998a,b; Lawton 2001; Pearson & Dawson 2003; Hampe 2004; Guisan & Thuiller 2005; Sax *et al.* 2007).

BOX 1. Key assumptions of bioclimatic models

- Biotic interactions are unimportant in determining geographic ranges or are constant over space and time.
- The genetic and phenotypic composition of species is constant over space and time.
- No dispersal limitation: species occur at all locations where climate is favorable and nowhere else.

Biotic interactions are unimportant in determining geographic ranges or are constant over space and time. In mechanistic bioclimatic models, where physiological tolerances measured in the laboratory are used to predict geographic ranges in the field, it is assumed that biotic interactions

are unimportant for species' distributions. Contrary to the wisdom of entire ecological subdisciplines, these models assume that realized ecological niches, which we see in the field, are not different from fundamental ecological niches measured in the laboratory (Hutchinson 1957). They assume that neither competition, mutualism, nor predation is important for species' distributions.

Empirical bioclimatic models make a softer assumption than mechanistic models on the influence of biotic interactions. Although they do not explicitly consider biotic interactions, their predictions are still valid if the influence of biotic interactions is constant over space and time. When an empirical model is parameterized for species occurrence data, the biotic interactions that caused these occurrence data are implicitly incorporated (the model should capture the species' realized niche). If the model is, for example, constructed to predict the future geographic range of an invader in an exotic continent, the crucial question is whether the influence of biotic interactions on this species' occurrence in the exotic continent is the same as in the native continent (does the realized niche remain the same?). Similarly, if the model is constructed to predict the temporal range shift due to climate change, the crucial question is whether the influence of biotic interactions will remain constant over space and time. Empirical models assume this to be the case.

Even this softer assumption of empirical bioclimatic models as compared to mechanistic models clearly contradicts ecological principles that are commonly outlined in textbooks (e.g., Begon *et al.* 2005). Biotic interactions do vary with space and time, for example because populations of competitors, mutualists, and predators vary with space and time. Voigt *et al.* (2003) showed that species from different trophic levels respond differently to climate change: the ranges of species within a given community are shifted unequally, hence the community and the biotic interactions are disrupted (see also Schmitz *et al.* 2003). Similarly, paleoecological studies report that plant communities with no present-day analogues were common in the

past, suggesting that novel climatic conditions in the future will also lead to no-analog communities. In other words, climate change may reshuffle communities and biotic interactions (Williams & Jackson 2007; Williams *et al.* 2007). Suttle *et al.* (2007) showed experimentally that biotic interactions can be more important than direct climate effects for species occurrences. With respect to invasive species, it is well known that biotic interactions differ between the native and exotic ranges of invaders. The enemy release hypothesis (Keane & Crawley 2002; Mitchell & Power 2003; Torchin *et al.* 2003) and EICA hypothesis (Evolution of Improved Competitive Ability; Blossey & Nötzold 1995; Withgott 2004) both say that species reaching higher densities in their exotic than their native range do so specifically because they face fewer enemies in their exotic range.

The genetic and phenotypic composition of species is constant over space and time. In both mechanistic and empirical bioclimatic models, it is assumed that the functional properties of species, that is, their phenotype and genotype, are constant over space and time. For example, when trying to predict paleoclimatic conditions based on a species' current and past distributions, a bioclimatic modeler assumes that this species has not changed during this long time period. When predicting range shifts due to global change, the modeler assumes that the new environment where the range has shifted to does not cause any genetic or phenotypic changes. And when predicting the potential range of an exotic species, it is additionally assumed that the few individuals that founded the population were genetically identical to the much larger source population.

Similarly to the first assumption of bioclimatic models, this second assumption ignores basic biological principles, in this case from the discipline of evolutionary biology. Evolutionary change does happen and sometimes even relatively fast. Ecological niches are often conservative (Peterson 2003), but especially when confronted with a new environment, species sometimes evolve rapidly (Davis & Shaw 2001; Cox 2004; Strayer *et al.* 2006;

Lockwood *et al.* 2007; Sax *et al.* 2007). Phenotypes change much faster than genotypes, but such nongenetic changes are again ignored by bioclimatic models. Phenotypic plasticity is of general importance (Karban & Baldwin 1997; Tollrian & Harvell 1999; DeWitt & Scheiner 2004) and might be especially pronounced in invaders (Daehler 2003; Strayer *et al.* 2006).

A good illustration of the problematic assumption that the genetic and phenotypic composition of species is constant over space and time is the frequent observation that invaders have larger body sizes in their exotic than their native range. For instance, the green crab (*Carcinus maenas*) has a 30% larger carapace width in its exotic than its native European range (Torchin *et al.* 2001). Since an individual's physiological tolerances critically depend on its body size, the size differences of many invaders between native and exotic range possibly relate to climatic niche differences and thus to serious errors in the exotic range predictions of bioclimatic models.

No dispersal limitation: species occur at all locations where climate is favorable and nowhere else. This third assumption also applies to both mechanistic and empirical models. Its first part, that species occur at all locations where climate is favorable, says that dispersal is unlimited, that is, that species have had the ability and sufficient time to populate all locations where climate is favorable. In fact, however, many species lack the means to reach suitable but distant locations, and species such as trees need long time periods to extend their range even to relatively close locations (Pearson 2006). Brown *et al.* (1996) put it as follows: "The success of introduced species in so many parts of the world indicates that many, probably most, species do not live everywhere they can" (pp. 614–615).

The second part of the above assumption says that species only occur at locations where climate is favorable. In other words, bioclimatic models ignore source–sink dynamics and assume that sinks do not exist. Metapopulation textbooks, such as Hanski (1999), include much evidence to the contrary.

Thus, bioclimatic models ignore a number of fundamental biological principles. It is generally unwise, however, to prejudge models based on their assumptions. Instead, their usefulness should be evaluated by means of performance tests against empirical data. We will come back to this point below.

Statistical Methods

In empirical bioclimatic models, various statistical approaches are used to predict a species' distribution based on climatic conditions (Box 2; for further, less frequently used approaches, see Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Heikkinen *et al.* 2006; and references in Table 1).

BOX 2. Statistical methods often used for empirical bioclimatic models

- Logistic regression, generalized linear model (GLM)
- Generalized additive model (GAM)
- Climate envelope (e.g., BIOCLIM)
- Classification and regression tree (CART)
- Neural network (NN), genetic algorithm (e.g., GARP)

Logistic regression analysis is a relatively straightforward technique to regress a binary response variable (presence/absence) against climatic variables. It has been used in many disciplines (e.g., medical, social, and biological sciences) and is thus well known and transparent. For general information, see for example Hosmer and Lemeshow (2000). Logistic regression models are generalized linear models (GLMs) with a logit link function, that is, for a binary response variable. In GLMs, the response variable is generally modeled as a linear function of the independent variables.

In generalized additive models (GAMs), the response variable is modeled as the additive combination of independent variables' functions, e.g., as smooth functions. This greater flexibility of GAMs allows a better data fit but comes with less transparency and

interpretability. See Hastie and Tibshirani (1990) for a general introduction to GAMs. General linear models and general additive models are widespread statistical techniques with many general applications.

Climate envelope techniques (e.g., ANUCLIM, BIOCLIM, DOMAIN, FEM, HABITAT, and Mahalanobis distance) are more specialized but also the classic bioclimatic modeling approach. They fit a minimal envelope in a multidimensional climate space and use presence-only instead of presence/absence data, which can be highly advantageous: many data sets provide presence-only data, and even if absence points are available, they are not always reliable, especially for areas that are not thoroughly inventoried or for species that are difficult to detect. On the other hand, if information on absence points is available and reliable, it is to a model's disadvantage not to employ it.

In classification and regression tree analysis (CART), the data set is recursively split into increasingly homogenous subsets with respect to the dependent variable, yielding a binary decision tree. The decision rules at the nodes use one or more of the independent variables. See Breiman *et al.* (1984) for more information.

Neural networks (NNs) and genetic algorithms are powerful approaches, but they are sometimes black boxes, so the models and predictions are often hard to interpret. Different NNs and genetic algorithms have been developed for bioclimatic models where the most widely used appears to be GARP (Genetic Algorithm for Rule-set Production; Stockwell & Peters 1999; Peterson 2001; Peterson & Vieglais 2001; Stockwell & Peterson 2002). Similar to climate envelope techniques, GARP does not need presence/absence data for its application, but presence-only data are sufficient.

A number of studies have compared the performance of these and other, less frequently used techniques (Table 1). It is not straightforward to summarize these studies, however, as they differ in several ways, for example with respect to criteria for model evaluation. The first difference relates to the data that the model prepa-

ditions are compared to, which can be classified into three groups (Fig. 1; Araújo *et al.* 2005): *resubstitution*—the model predictions are compared to the same data used to fit the model; *data splitting*—the data are split into a training set used to fit the model and a validation set used to evaluate the model (jackknifing, bootstrapping, and cross-validation belong to this category); or *independent validation*—the models are fitted with data set A and compared to a spatially or temporally independent data set B, from a nonadjacent region or different time period. Here, we arbitrarily decided to count data sets as temporally independent if they differed by at least 15 years (ideally, this time period should depend on the focal species).

Independent validation is preferable for most applications, followed by data splitting and resubstitution. The accuracy measures given by data splitting and especially resubstitution can be inflated due to overfitting. Only independent validation tests the kind of model predictions that we usually want: if our goal is to evaluate model predictions on range shifts due to climate change, the models should be evaluated against observed range shifts, for instance, by fitting them to historical data and comparing them to current data. Similarly, if we evaluate predictions on an invader's exotic range, we should fit the models to data from the species' native range and compare them to data from its exotic range. Independent validation, however, was applied in only three of the 33 studies listed in Table 1 (we will come back to this point in the section *Frontiers*). Those studies that applied two or all three of the evaluation methods show that the ranking of modeling techniques often depends on the evaluation method that is used.

Once it is clear which data should be compared to model predictions, the second question is how to compare them, that is, which measure of model performance to use. The most appropriate evaluation metric depends on the goals of the modeling exercise and the characteristics of the model output (e.g., binary versus continuous), so it is not surprising that different authors have used different metrics. The most commonly used ones are Cohen's kappa

TABLE 1. Studies comparing the performance of different statistical methods

Study	Species	Evaluation method	Modeling techniques' ranking ¹
Studies that tested the models by means of resubstitution (cf. Fig. 1)			
Walker (1990)	Kangaroos ($N = 3$ species)	False positives, false negatives ^{2*}	CART > GLM
Skidmore <i>et al.</i> (1996)	Kangaroos ($N = 3$)	Proportion of correct predictions*	CART > BIOCLIM > SNPC
Mastrorillo <i>et al.</i> (1997)	Fish ($N = 3$)	Proportion of correct predictions ^{3*}	NN > DA ⁴
Bio <i>et al.</i> (1998)	Plants ($N = 156$)	χ^2 *	GAM > GLM
Franklin (1998)	Plants ($N = 20$)	Residual deviance, false positives, false negatives*	CART > GAM > GLM
Loiselle <i>et al.</i> (2003)	Birds ($N = 11$)	Kappa*	DOMAIN > Simple overlay > GARP > GLM > BIOCLIM
Segurado and Araújo (2004)	Amphibians, reptiles ($N = 44$)	Sensitivity, ⁵ kappa*	NN > GAM > CART \approx GLM > Spatial interpolation > BIOMAPPER \approx DOMAIN
Studies that tested the models by means of data splitting			
Manel <i>et al.</i> (1999)	Birds ($N = 6$)	Proportion of correct predictions* Proportion of correct predictions, sensitivity, specificity, kappa, among others**	NN > DA > GLM GLM > DA > NN
Vayssières <i>et al.</i> (2000)	Oaks ($N = 3$)	Sensitivity, specificity, ⁶ differential positive rate ^{7**}	CART > GLM
Elith and Burgman (2002)	Plants ($N = 8$)	Area Under receiver operating characteristic Curve (AUC)* AUC**	GARP > GAM > GLM > ANUCLIM GAM > GLM > GARP > ANUCLIM
Fertig and Reiners (2002)	<i>Mentzelia pumila</i>	True positives, true negatives, false positives, false negatives*,**	CART \approx GLM
Olden and Jackson (2002)	Fish ($N = 27$), artificial species ($N = 2$)	Proportion of correct predictions, sensitivity, specificity**	NN > CART \approx DA \approx GLM
Stockwell and Peterson (2002)	Birds ($N = 103$)	Proportion of correct predictions**	GARP > GLM; performance of coarse and fine surrogate models heavily depend on sample size
Farber and Kadmon (2003)	Woody plants ($N = 192$)	Proportion of correct predictions, sensitivity, specificity, kappa**	Mahalanobis distance > BIOCLIM
Thuiller (2003)	Trees ($N = 61$)	AUC, kappa* AUC, kappa**	NN > GAM > GLM > CART NN > GAM > CART > GLM
Thuiller <i>et al.</i> (2003)	Trees ($N = 4$)	AUC**	GAM > GLM > CART

Continued

Table 1. Continued

Study	Species	Evaluation method	Modeling techniques' ranking ¹
Muñoz and Felicísimo (2004)	<i>Grimmia</i> spp., <i>Fagus sylvatica</i>	AUC**	CART ≈ MARS > GLM
Robertson <i>et al.</i> (2004)	Plants ($N = 3$), cicadas ($N = 3$)	Kappa**	FEM > BIOCLIM
Johnson and Gillingham (2005)	<i>Rangifer tarandus caribou</i>	r, r_s **	Mahalanobis distance > GLM > GARP > HSI
Elith <i>et al.</i> (2006)	Animals, plants ($N = 226$)	AUC, correlation, kappa**	BoostedRT ≈ MARS-COMM > GDM ≈ Maxent > GAM > GLM > DOMAIN ≈ GARP > BIOCLIM ≈ LIVES
Hernandez <i>et al.</i> (2006)	Animals ($N = 18$)	AUC, sensitivity, area predicted present, kappa**	Maxent > DOMAIN > GARP > BIOCLIM
Lawler <i>et al.</i> (2006)	Mammals ($N = 100$)	AUC, sensitivity, specificity, kappa**	Random forests > GLM > GAM ≈ NN > CART ≈ GARP
Pearson <i>et al.</i> (2006)	Proteaceae ($N = 4$)	AUC, kappa**	GAM ≈ NN > GLM > DOMAIN > CART > GA > GARP > BIOCLIM
Phillips <i>et al.</i> (2006)	Mammals ($N = 2$)	Extrinsic omission rate, proportional predicted area, AUC**	Maxent > GARP
Randin <i>et al.</i> (2006)	Plants ($N = 54$)	AUC, kappa**	GAM ≈ GLM
Schussman <i>et al.</i> (2006)	<i>Eragrostis lehmanniana</i>	Sensitivity, specificity, kappa**	GLM > GARP
Zeman and Lynen (2006)	<i>Rhipicephalus appendiculatus</i>	Mean squared difference**	Weights of evidence (Bayesian) > GAM > DA
Meynard and Quinn (2007)	Artificial species ($N = 18$)	AUC, sensitivity, specificity, kappa, correlation true/predicted prob. of occurrence**	GAM > GLM > CART > GARP
Peterson <i>et al.</i> (2007)	Birds ($N = 3$)	AUC**	Maxent > GARP
Tsoar <i>et al.</i> (2007)	Animals ($N = 42$)	Kappa**	GARP > Mahalanobis distance > HABITAT > DOMAIN > BIOCLIM > ENFA
Studies that tested the models by means of independent validation			
Dettmers <i>et al.</i> (2002)	Birds ($N = 6$)	Proportion of correct predictions**	DA > CART > GLM > Mahalanobis distance
		Proportion of correct predictions***	CART > Mahalanobis distance > GLM > DA
Araújo <i>et al.</i> (2005)	Birds ($N = 116$)	AUC, kappa*	NN > GAM ≈ GLM ≈ CART
		AUC, kappa**	NN > GAM ≈ GLM > CART
		AUC, kappa***	NN > GAM > GLM ≈ CART

Continued

Table 1. Continued

Study	Species	Evaluation method	Modeling techniques' ranking ¹
Broennimann <i>et al.</i> (2007)	<i>Centaurea maculosa</i>	AUC** AUC***	Random forests > BoostedRT > GAM \approx MARS > GLM > MixtureDA > NN > CART GAM > MixtureDA > Random forests > GLM > CART > MARS > NN > BoostedRT

¹The rankings represent significant differences or trends. We decided not to exclusively rely upon significant differences in order to allow for a better comparison of the studies. ²True positives are correctly predicted presences, true negatives are correctly predicted absences, false positives are predicted presences where absences are observed, and false negatives are predicted absences where presences are observed. ³Proportion of correct predictions = (number of true positives + number of true negatives)/(number of true positives + number of true negatives + number of false positives + number of false negatives). ⁴DA denotes discriminant analysis. ⁵Sensitivity (proportion of true positives correctly predicted) = number of true positives/(number of true positives + number of false negatives). ⁶Specificity (proportion of true negatives correctly predicted) = number of true negatives/(number of true negatives + number of false positives). ⁷Differential positive rate = sensitivity - (1 - specificity). *Resubstitution. **Data splitting. ***Independent validation.

(used in 15 studies) and AUC (Area Under receiver operating characteristic Curve; used in 14 studies. There is an ongoing debate on the best measures, but we cannot go into detail here and refer interested readers to the literature (Fielding & Bell 1997; Guisan & Zimmermann 2000; Pearce & Ferrier 2000; Manel *et al.* 2001; Fielding 2002; Liu *et al.* 2005; Vaughan & Ormerod 2005; Allouche *et al.* 2006).

The overall picture painted by Table 1 is that no modeling technique consistently outperforms other techniques. The findings of the different studies are highly variable, but the most recent comparisons suggest that new techniques—including the model-averaging random forests (Lawler *et al.* 2006; Broennimann *et al.* 2007) and the Bayesian weights-of-evidence model (Zeman & Lynen 2006)—outperform more established methods. On the other hand, since these techniques have only been included in a few comparative studies, it is currently impossible to estimate their general predictive power. Of the more classic methods outlined above—GLM, GAM, and climate envelope—GAM usually performs best, followed by GLM, and climate envelope techniques rank in third place. Mixed results have been reported for CART and NNs, but the latter have performed relatively well overall, sometimes surpassing GAM. The perfor-

mance of the widely used GARP appears to be intermediate. In conclusion, the choice of method will always depend on the focal species, data set, and question, but given that the newest techniques often achieve the most accurate predictions and that more techniques are constantly being developed, it remains to be seen if one or a few techniques can excel for most applications.

What Is It Done For? Applications of Bioclimatic Modeling

Bioclimatic models have come into wide use in ecology in recent years and have been applied to a broad range of ecological problems, both basic and applied (Manel *et al.* 2001; Guisan & Thuiller 2005; Peterson 2006). The following brief survey covers their major uses.

Predicting the Future

Bioclimatic models are the most important tool now used to predict future changes in the geographic ranges of species. The two most common applications are predicting shifts in geographic ranges in response to anthropogenic climate change and the establishment or spread of invasive species after they are introduced into new regions by humans.

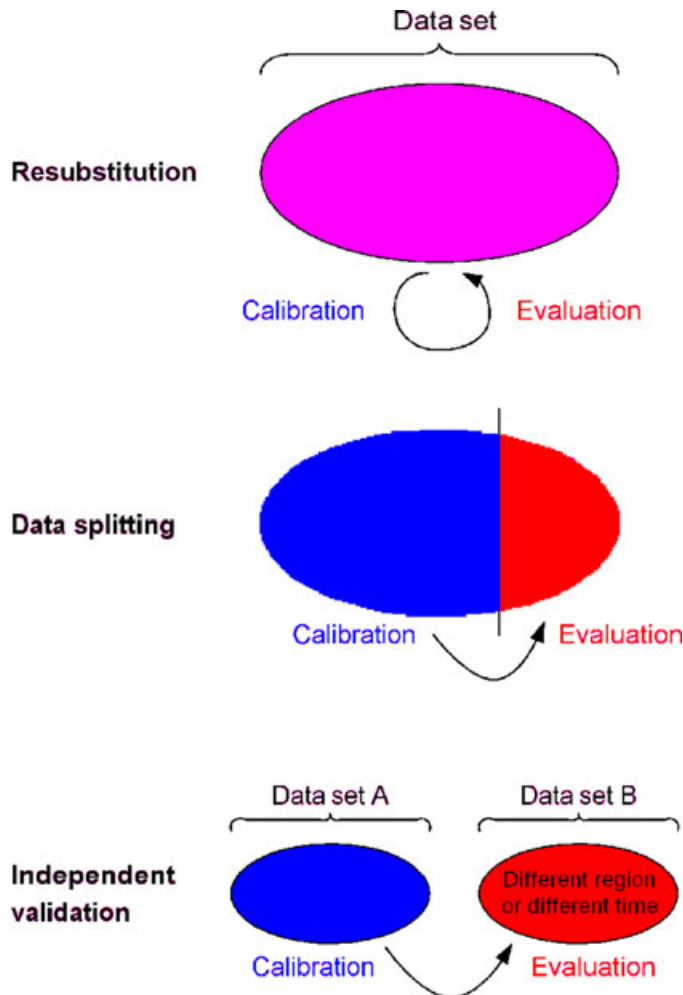


Figure 1. Different strategies of model validation. (In color in *Annals* online.)

Predicting Responses to Climate Change

Bioclimatic models often are coupled to climate-change models to predict how the geographic ranges of species will shift as anthropogenic climate change proceeds (e.g., Lindenmayer *et al.* 1991; Brereton *et al.* 1995; Oberhauser & Peterson 2003; Peterson *et al.* 2004a; Roura-Pascual *et al.* 2004; Araújo *et al.* 2005; Bomhard *et al.* 2005; Thuiller *et al.* 2005a,b; Walther *et al.* 2005; Téllez-Valdés *et al.* 2006; Lima *et al.* 2007; Nunes *et al.* 2007; Williams *et al.* 2007). The goal is typically to predict the range (or survival) of species, but it may also be to compare the biological effects of different climate-change scenarios. A wide range of species have been treated by these models, including economically or ecologically impor-

tant species such as crops, valuable species that are harvested from the wild (e.g., timber, sport fishes), pests, diseases, biocontrol agents, foundation or keystone species, and imperiled species (Lindenmayer *et al.* 1991; Brereton *et al.* 1995; Roura-Pascual *et al.* 2004; Araújo *et al.* 2005; Bomhard *et al.* 2005; Parra-Olea *et al.* 2005; Téllez-Valdés *et al.* 2006; Nunes *et al.* 2007).

Thus, Thuiller *et al.* (2005b) used bioclimatic models to derive several important insights about how climate change might affect the local (i.e., a 50 × 50 km grid) composition of plant communities in Europe. They suggested that climate change would cause both local losses and gains of plant species, that these changes could be large, and that there would

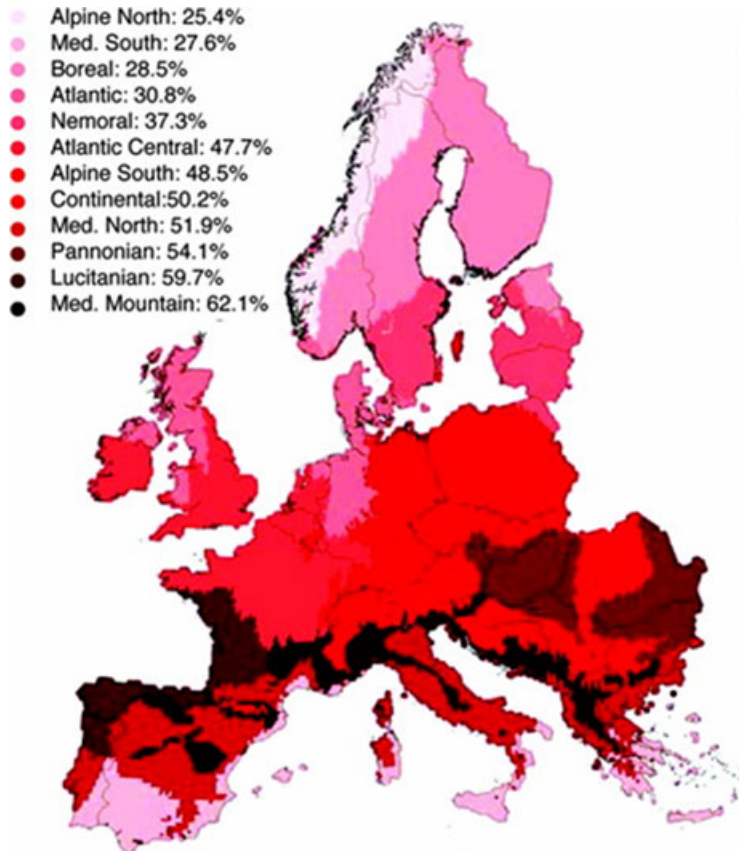


Figure 2. Effects of climate change on local plant communities in various biogeographic regions of Europe. The map shows the estimated percentage of the plant species that currently occur in a 50×50 km pixel that would be lost from that pixel as a result of one specific climate-change scenario (from Thuiller *et al.* 2005b; copyright 2005 National Academy of Sciences, U.S.A.). (In color in *Annals* online.)

be large regional differences in the severity of change (Fig. 2). They also found that predictions differed across climate-change scenarios, and that dispersal rates of plants could strongly influence how plant communities changed.

Conservationists have begun to couple bioclimatic models to spatially explicit information on the distribution of reserves or threats (typically land-use change) to ask how the spatial structure of the real world affects the response of species to climate change (Araújo *et al.* 2004; Bomhard *et al.* 2005; Parra-Olea *et al.* 2005; Téllez-Valdés *et al.* 2006; Hannah *et al.* 2007). Not surprisingly, such models suggest that climate change will complicate efforts to protect species and should be taken into account in cur-

rent conservation planning. For instance, Hannah *et al.* (2007) concluded that existing reserve networks were unlikely to conserve all species of interest through a period of climate change, and that early planning could substantially reduce the area of reserves necessary to protect species.

Predicting Ranges of Invasive Species

Because invasive species cause ecological and economic damages (Mack *et al.* 2000; Lodge *et al.* 2006; Lockwood *et al.* 2007), many ecologists have used bioclimatic models to project the future ranges of alien species. These projections are used to assess the risk associated with the establishment of new aliens, to demonstrate

the need for import controls on potential pest species (Panetta & Mitchell 1991), or to target management actions to control these species (Peterson & Robins 2003). Bioclimatic models for invasive species have been run for small regions (Iguchi *et al.* 2004, Underwood *et al.* 2004; Guo *et al.* 2005; Anderson *et al.* 2006), continents (Strayer 1991; Sindel & Michael 1992; Beerling *et al.* 1995; Martin 1996; Peterson *et al.* 2003, 2004b, 2006a; Drake & Bossenbroek 2004; Drake & Lodge 2006; Zambrano *et al.* 2006; Chen *et al.* 2007; Fitzpatrick *et al.* 2007; Herborg *et al.* 2007; Loo *et al.* 2007), and the entire globe (Roura-Pascual *et al.* 2004; Ron 2005; Thuiller *et al.* 2005c; Li *et al.* 2006; Mohamed *et al.* 2006; Raimundo *et al.* 2007). Box 3 describes how the range of the invasive zebra mussel (*Dreissena polymorpha*) has been predicted in North America by means of bioclimatic modeling.

Figure 3 shows another example of the use of a bioclimatic model to predict the range of an invasive species in a new continent, and also illustrates the critical importance of careful evaluation of model performance. Loo *et al.* (2007) used GARP to predict the potential range of an invasive freshwater snail (*Potamopyrgus antipodarum*) in North America. Models based on its native distribution in New Zealand produced satisfying fits for New Zealand (AUC = 0.73) but seriously underpredicted the range that the species has already achieved in North America. Models based on these existing North American occurrences predicted a much wider potential range of this species in North America. The large discrepancy between the two models has significant implications for the management and eventual impacts of this species.

Bioclimatic models also have been used to assess whether the current range of a well established alien is likely to increase in the future as it fills out its range (Martin 1996; Zambrano *et al.* 2006) or responds to anthropogenic climate change (Roura-Pascual *et al.* 2004). Herborg *et al.* (2007) combined the output from a bioclimatic model with estimates

of ballast water releases at various ports to identify the entry points at which the Chinese mitten crab (*Eriocheir sinensis*) was most likely to invade, a problem with obvious utility for monitoring and management programs.

Understanding the Present

Bioclimatic models also are widely used to describe or interpret present-day species distributions, or to address current management problems.

Investigating Mechanisms Underlying Geographic Ranges

Bioclimatic models have been used to investigate the roles of climate and other variables in setting the geographic ranges of species (Law 1994; Manning *et al.* 2005; Rees *et al.* 2007). They may be run to see whether a particular value of a specific climatic variable hypothesized to be important in range bounding, or indeed any climatic variable, coincides with the actual range boundary of a species. If the range boundary lines up with a climatic variable, that variable is interpreted as controlling the range boundary. If no climatic variable coincides with the range boundary, then nonclimatic variables are thought to be important. Ecologists have been particularly interested in whether climatic variables or other causes are responsible for disjunctions in species ranges, or whether large areas of suitable climate exist that fail to support a species for other reasons.

Describing the Actual Range from Sparse Survey Data

The actual geographic range of a species may be poorly known, especially if the species is cryptic in habit or has received little study. Bioclimatic models based on incomplete distributional information have been widely used to infer the full geographic range of the species (Walther *et al.* 2004; Pearson *et al.* 2007; and references listed below). This exercise has many applications. The models can be used to guide

surveys for rare or valuable species in hitherto unsampled areas (Lindenmayer *et al.* 1991; Villordon *et al.* 2006; Pearson *et al.* 2007). Estimates of the actual range of a species can be compared to the distribution of protected areas to assess whether the species is adequately protected (Gaubert *et al.* 2006; Irfan-Ullah *et al.* 2007). Conservation assessments of rare species typically require information on the geographic range of the species (IUCN 2007), which can be estimated by bioclimatic modeling (Sérgio *et al.* 2007). Fine-scale estimates of actual ranges de-

rived from bioclimatic models have been used as the basis of statistical analyses of the controls on species distributions or richness (White & Kerr 2007), or to identify areas of endemism (Escalante *et al.* 2007). Bioclimatic models have even been used to predict the geographic distribution of diseases that are rare, such as Marburg hemorrhagic fever (Peterson *et al.* 2006b) and monkeypox (Levine *et al.* 2007), or for which the geographic range of vectors is poorly known (Peterson *et al.* 2004c; Adjemian *et al.* 2006).

BOX 3. A case study: predicting the range of the invasive zebra mussel (*Dreissena polymorpha*) in North America.

- The appearance of the zebra mussel in North America in 1988 raised two critical questions: How bad will its impacts on freshwater ecosystems and infrastructure be? And how far will it spread? Bioclimatic models have been important in answering the latter question.
- Because zebra mussels are so widespread in Europe, even the earliest papers on its appearance in North America (Hebert *et al.* 1989; Roberts 1990) noted that it might spread widely in North America. McMahon and Tsou (1990) made the first attempt to define its potential range more precisely. Applying results from laboratory studies on thermal tolerances of the species, they produced a rough map suggesting that the species might occupy a broad range from just north of the U.S.–Canada border to about the southern tier of states in the United States (see Figure for Box3). About the same time, Strayer (1991) developed formal bioclimatic models for the species based on its distribution in Europe and a suite of bioclimatic variables. Although both the climatic variables (terrestrial climate variables collected from paper records) and the statistical analysis (discriminant analysis) would be considered primitive by modern standards, these models again showed the potential for zebra mussels to occupy a large range in North America. They also identified two key informational gaps. First, Strayer's analysis suggested that the European range of the zebra mussel was not climate limited, so that any geographic ranges projected from its European distribution would have to be interpreted as minima (a caveat often overlooked by people who cite this paper!). Second, although zebra mussel larvae require high levels of dissolved calcium to survive and develop, there were not good databases on environmental calcium concentrations that could be included in the models. It was clear that adding calcium to the models would severely reduce the projected range of the species in North America.
- The next large advance in projecting the broad distribution of this species in North America did not come until 2004, when Drake & Bossenbroek applied GARP models (based on the realized range of zebra mussels in North America, rather than European records) to project the range of zebra mussels in North America. These models included more variables (climate, hydrology, geology) than Strayer's models, operated at a finer spatial scale, and produced much more detailed projections of the potential North American range than earlier models. Nevertheless, Drake & Bossenbroek's models still did not address calcium limitation very well. On the other hand, another recent model (Whittier *et al.* 2008) was based solely on environmental calcium concentrations, but did not include any climatic data, and produced correspondingly different predictions for the range, especially in New England, the Southeast, and the Pacific Northwest.
- Any of these models is sufficient to identify the potential of zebra mussels to spread widely in North America, and they are used widely by scientists and managers. The earliest models did not produce any formal predictions for local occurrence of zebra mussels, and it remains to be seen how well the most recent models will meet the needs of managers to predict local details of the geographic range. It is

unfortunate that there has been very little rigorous comparison of models (but see Drake & Bossenbroek 2004, for an illuminating exception), nor any effective combination of climate and calcium into a single model. Finally, it is curious that the most recent models exclude Canada, which is after all where the species was first detected!

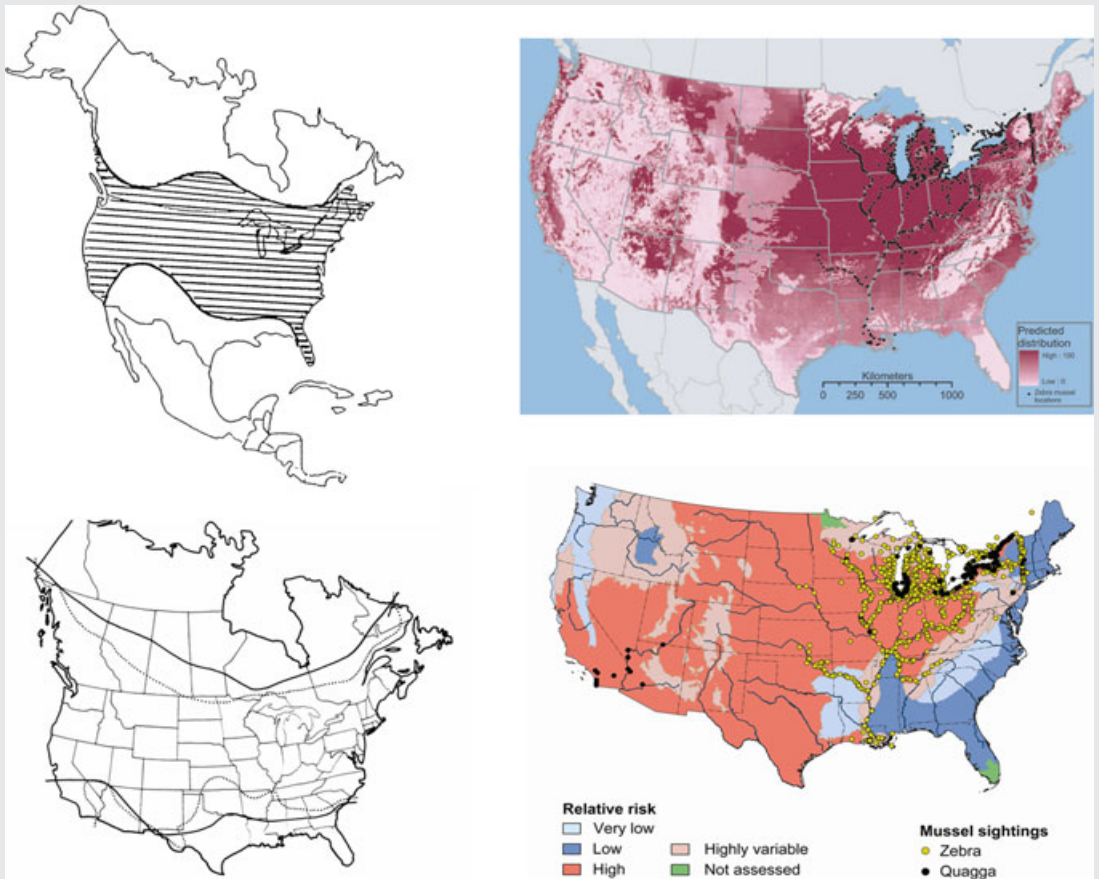


Figure for Box 3. Evolution of models to predict the geographic range of zebra mussels in North America. *Upper left:* McMahon and Tsou's (1990; copyright 1990 PennWell Corporation) model, based largely on thermal tolerances measured in the laboratory. *Lower left:* range limits from two of Strayer's (1991) projections, based on different thermal limits inferred by discriminant analysis from the European range of the species. *Upper right:* predictions from one of Drake and Bossenbroek's (2004; copyright, American Institute of Biological Sciences) GARP models, based on the realized distribution of the species in North America. Darker shades show higher likelihood of invasion, and dots show localities from which the species was known as of 2003. *Lower right:* predictions from Whittier *et al.* (2008; copyright 2008 Ecological Society of America), based on environmental calcium concentrations. Dots show sites from which *Dreissena* spp. had been observed as of October 2007. (In color in *Annals* online.)

Identifying Suitable Sites for the Stocking or Culture of Valuable Species

Humans often deliberately move valuable species outside of their native range for agri-

culture, forestry, fisheries, or biological control. Bioclimatic models have been used to identify suitable sites at which to stock or grow such species, or to evaluate the reasons behind stocking failures (Richardson & McMahon 1992;

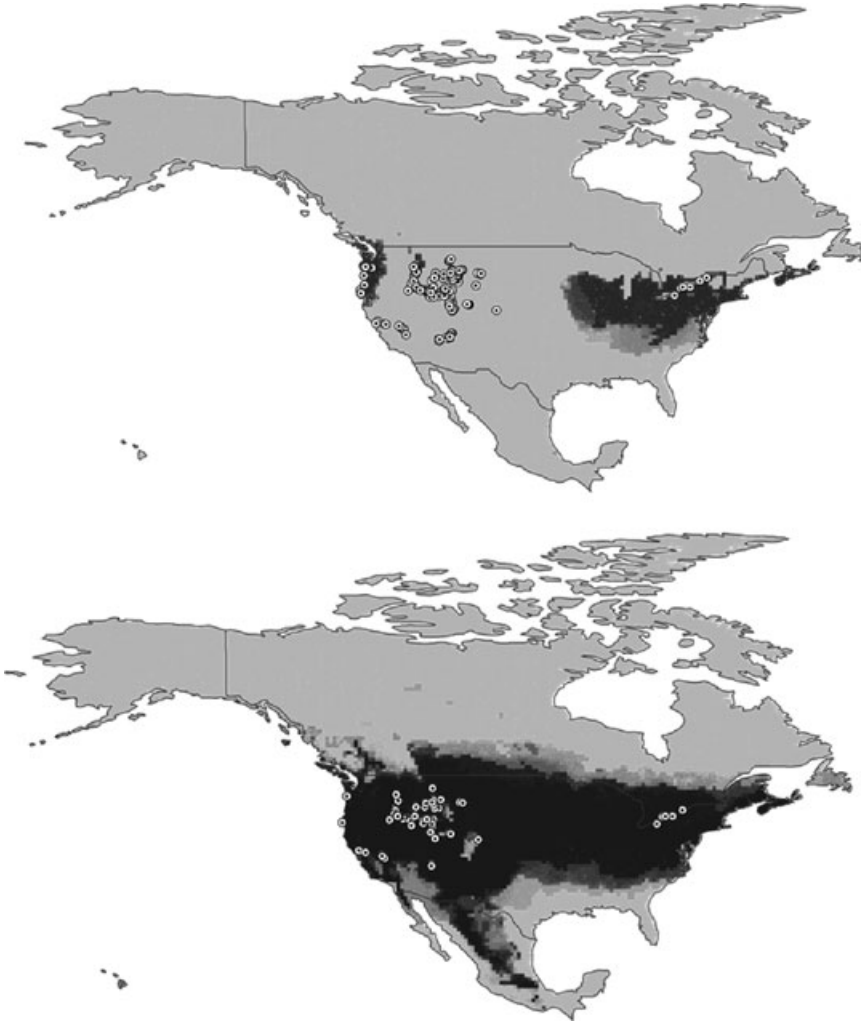


Figure 3. Potential range of the invasive freshwater snail *Potamopyrgus antipodarum* in North America based on (upper) its native range in New Zealand or (lower) its existing range in North America (from Loo *et al.* 2007; copyright 2007 Ecological Society of America). Shading shows the proportion of best subset GARP models that predict the occurrence of the species, with darker shades showing areas where more models predict occurrence. Circles show known point occurrences of *P. antipodarum* in North America.

Cunningham *et al.* 2002). In a related application, scientists searching for suitable biocontrol agents for pest species or germplasm for crops have used bioclimatic models to locate suitable source areas which might be explored to find climatically well adapted populations (Fiaboe *et al.* 2006; Villordon *et al.* 2006). It is interesting to note that scientists using bioclimatic models for these purposes sometimes observe

that a species can be established successfully outside its bioclimatic niche as defined from its native range (e.g., Richardson & McMahon 1992).

Clarifying Systematic Relationships

Finally, ecological information derived from bioclimatic models has been used to bolster conclusions of taxonomic studies about the

distinctness of different populations that might represent cryptic species (Fischer *et al.* 2001). The assumption here is that different species would have different climatic niches, so if two groups of populations from different regions are shown to have different bioclimatic niches, they are likely to be different species or subspecies.

Reconstructing the Past

Paleoecologists have long used biotic distributions to infer paleoclimates, either formally with various models, or informally. Bioclimatic models have recently been used to assist in these paleoclimatic inferences (Kershaw 1997; Kinzelbach *et al.* 1997; Dimitriadis & Cranston 2001; Marra *et al.* 2004; van der Kaars *et al.* 2006; Ramstein *et al.* 2007). They have also been used to reconstruct conditions in the recent past. For instance, it is difficult to know how much anthropogenic activities have reduced range sizes for the many species whose historic ranges are poorly known. In such cases, bioclimatic models can be used to reconstruct past ranges, against which current, known ranges can be compared to estimate range reductions (Bond *et al.* 2006). Alternatively, climatic data can be combined with land-use data to estimate both past and present ranges to estimate range reductions (Peterson *et al.* 2006c; Rees *et al.* 2007).

Does It Make Us Wiser? General Contributions of Bioclimatic Modeling

Bioclimatic models have made several important general contributions to ecology. Most obviously, they have been a rich source of quantitative projections or hypotheses concerning the geographic ranges of species. These projections or hypotheses are potentially of great value in many areas of both basic and applied ecology, and are especially valuable because ecologists have so few practical tools with which to address these important questions. Because



Figure 4. The present-day range of the black tufted-ear marmoset (*Callithrix penicillata*) as predicted by the random forests model and compared to the observed range (from Lawler *et al.* 2006; copyright 2006 Lawler *et al.*, Blackwell Publishing Ltd.). (In color in *Annals* online.)

of limited testing with respect to the various applications, however, the general usefulness of bioclimatic models is currently unclear. We will come back to this important point in the next section, *Frontiers*.

Bioclimatic models have shown considerable abilities to fit even complicated geographic ranges (Fig. 4), where the ranges of species with narrow niches in climate space tend to be modeled more successfully than those with broader niches (Kadmon *et al.* 2003; Tsoar *et al.* 2007). There has been some concern that bioclimatic models might perform poorly for species that have very slow dispersal (Stockman *et al.* 2006) or are highly mobile (such species might be seen passing through habitats that are not capable of supporting the species over the long term; Manning *et al.* 2005), but these issues have not been fully resolved.

The general ability of bioclimatic models to fit geographic ranges has reinforced the ancient notion that climatic variables often exert a primary control on the geographic ranges

of most species. This conclusion must be interpreted very cautiously, however, for several reasons. First, species occur outside the ranges predicted by bioclimatic models (e.g., Richardson & McMahon 1992; Loo *et al.* 2007), suggesting that nonclimatic factors are of primary importance in setting some range boundaries. Additionally, there have been few tests of bioclimatic models using freshwater or other poorly dispersing organisms for which dispersal rather than climate might be expected to set range boundaries. Further, the coincidence of a range boundary with an isoline of some climatic variable is not enough to demonstrate that the climatic variable sets the range boundary, although it suggests a hypothesis that could be tested by a more rigorous method. Finally, even if the performance of bioclimatic models is interpreted as evidence that climate is important in setting geographic ranges, the considerable variation in species distributions that is not explained by these models shows that there is ample room for other factors (biological interactions, dispersal) to be important as well.

Bioclimatic models have made essential contributions to the scientific and public discussion about the ecological effects of anthropogenic climate change by providing quantitative scenarios and visualizations (e.g., Fig. 2). Even if these scenarios cannot always be regarded as literal predictions of the future, they certainly show that climate change is likely to cause large shifts in biotic distributions, that climate change will interact strongly with other anthropogenic drivers such as land-use change (Araújo *et al.* 2004; Bomhard *et al.* 2005; Parra-Olea *et al.* 2005; Téllez-Valdés *et al.* 2006; Hannah *et al.* 2007), and that conservation planning and reserve design will need to take climate change into account (e.g., Hannah *et al.* 2007). Another applied issue addressed by bioclimatic models is the pressing problem of invasive species, including diseases. Bioclimatic models have shown that most invasive species have considerable unrealized potential to spread (along with their ecological and economic impacts) (e.g., Fig. 3 and references cited above), as long as humans

continue to be careless about providing these species with transport opportunities. Finally, bioclimatic models have been helpful in conservation planning and surveys for rare species by providing estimates of actual geographic ranges from sparse survey data. Although it might be argued that we didn't need a model to tell us that anthropogenic climate change would affect species ranges or that invasive species pose ecological and economic threats, the quantitative output and powerfully evocative maps produced by bioclimatic models (Figs. 2 and 3) have lent weight and urgency to discussions of these issues.

Finally, bioclimatic modeling has brought a number of sophisticated statistical modeling techniques to ecology (see section *Statistical Methods*). Methods used for bioclimatic modeling have obvious utility for habitat modeling in general, as well as other ecological applications. Further, the increasingly sophisticated discussion about evaluating the performance of bioclimatic models (Fielding & Bell 1997; Guisan & Zimmermann 2000; Pearce & Ferrier 2000; Manel *et al.* 2001; Fielding 2002; Liu *et al.* 2005; Vaughan & Ormerod 2005; Alouche *et al.* 2006) has the potential to substantially improve the interpretation of models with binary output, which are widely used in ecology.

What Are the Major Obstacles and Needs? Frontiers

Bioclimatic Models Are Often Applied but Rarely Tested

The testing and evaluation of bioclimatic models need to be tied more closely to their specific intended uses. Two issues deserve more careful attention: the degree of fit between the model and the test data, and the type of data that are used to evaluate the model. Many studies have judged model performance using weak criteria (e.g., simply whether the model performs better than random) that do not show how useful the model will be for a particular application. The metric used to judge a model

(e.g., AUC, Cohen's kappa, true skill statistic, sensitivity, specificity) and the value of that metric needed to demonstrate that a model is useful both depend entirely on the intended uses of the model. Just as there is no special value of r^2 that shows that a linear regression is adequate, there will be no single value of AUC or kappa that shows that a bioclimatic model is adequate for all purposes.

The appropriate data for testing a model likewise depend on the intended use of the model (Fig. 1). If a bioclimatic model is intended to identify a species' present-day range based on sparse survey data (see section *What is it done for?*), it may be sufficient to evaluate model performance by splitting the data into a training set used to fit the model and a validation set used to evaluate the model. Such tests have been done frequently. Thus, studies given in Table 1 that applied this evaluation method reported an average value of 0.85 ± 0.029 (SE; $N = 12$) for AUC, where a random predictor has a value of 0.5, a perfect predictor achieves 1, and a value ≥ 0.9 is usually taken to indicate high accuracy (Swets 1988; Manel *et al.* 2001; Araújo *et al.* 2005; Pearson *et al.* 2006; Randin *et al.* 2006). For kappa, the average value of studies listed in Table 1 is 0.52 ± 0.065 (SE; $N = 12$); here, a random predictor has a value of 0, a perfect predictor achieves 1, and the benchmark for high accuracy is 0.7–0.75 (Monserud & Lee-mans 1992; Fielding & Bell 1997; Araújo *et al.* 2005; Pearson *et al.* 2006; Randin *et al.* 2006). While in a general sense these metrics suggest that bioclimatic models of present-day ranges perform satisfactorily, only an individual model user can really say whether these values of AUC or kappa are high enough (or indeed, whether AUC or kappa are the appropriate metrics).

For most applications of bioclimatic modeling, especially for predicting range shifts due to climate change or the spread of invaders, model performance should be tested by means of independent validation, rather than resubstitution or data splitting (cf. Fig. 1). It is usually difficult to locate such independent data sets, so studies that apply this method are currently the

exception (Box 4). A number of paleoecological studies evaluated bioclimatic models based on inferred past climatic conditions (Prentice *et al.* 1991; Martínez-Meyer *et al.* 2004; Martínez-Meyer & Peterson 2006; Ramstein *et al.* 2007). This is the best one can do if past climatic conditions are unknown, but we do not list such model evaluations in Box 4, as they are less reliable and not directly comparable to evaluations based on measured climate data. Most of the studies in Box 4 only evaluated the models against random predictions or did not calculate any objective evaluation measure. Only a few calculated gradual quantitative evaluation measures: Araújo *et al.* (2005), Lima *et al.* (2007), Loo *et al.* (2007), and Broennimann *et al.* (2007) reported AUC values of 0.80, 0.73, 0.61, and 0.50 on average, respectively; Walther *et al.* (2005) and Araújo *et al.* (2005) reported kappa values of 0.50 and 0.42, respectively; and Dettmers *et al.* (2002) reported an average proportion of correct predictions of 0.55. As expected, these metrics suggest that bioclimatic models perform less successfully when training data and test data are spatially or temporally independent than if both are from the same region and time. But again, whether these metrics indicate satisfactory model performance depends on the needs of the model user.

BOX 4. Studies that tested bioclimatic models by means of independent validation (cf. Fig. 1)

- Predicting the future
Climate change: Araújo *et al.* (2005), Walther *et al.* (2005), Lima *et al.* (2007), Nunes *et al.* (2007)
Invaders: Beerling *et al.* (1995), Peterson and Vieglais (2001), Peterson *et al.* (2003), Thuiller *et al.* (2005c), Broennimann *et al.* (2007), Fitzpatrick *et al.* (2007), Loo *et al.* (2007)
- Understanding the present: Dettmers *et al.* (2002)
- Reconstructing the past: Kinzelbach *et al.* (1997), Hill *et al.* (1999).

Extending Bioclimatic Models

In spite of the scarcity of information, we may cautiously conclude from the last section that bioclimatic models, especially for projecting range shifts due to climate change or the spread of invaders, need further improvement before they reliably lead to excellent or even good predictions. An important step towards this goal may be taken by considering the above-mentioned key assumptions of bioclimatic models (section *How is it done?*). Some studies already extended the current modeling approach by considering species interactions (Leathwick & Austin 2001; Anderson *et al.* 2002; Leathwick 2002; Araújo & Luoto 2007; Heikkinen *et al.* 2007; Sutherst *et al.* 2007). Dispersal limitation has sometimes been included by an assumed maximum dispersal distance (Midgley *et al.* 2006; Williams *et al.* 2007) or by simply assuming that climatically suitable areas that lie beyond obstacles such as mountains are not within the potential range of the species (Peterson *et al.* 2006c; Irfan-Ullah *et al.* 2007); only a few studies applied more complex dispersal models (Carey 1996; Iverson *et al.* 2004). It would be important to continue this work on extended bioclimatic models and then rigorously test the models by means of independent validation, also in comparison to ordinary bioclimatic models in order to learn how much is gained by considering species interactions or dispersal limitation. The limited knowledge we have so far suggests that the gain can be substantial.

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Conflicts of Interest

The authors declare no conflicts of interest.

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