Methods and uncertainties in bioclimatic envelope modelling under climate change

Risto K. Heikkinen,[1]* Miska Luoto,[1]
Miguel B. Araújo,[2,3] Raimo Virkkala,[1]
Wilfried Thuiller[3,4] and Martin T. Sykes[5]

[1]Finnish Environment Institute, Research Department, Research Programme for Biodiversity, PO Box 140, FIN-00251 Helsinki, Finland
[2]Department of Biodiversity and Evolutionary Biology, National Museum of Natural Sciences, CSIC, Madrid, Spain
[3]Macroecology and Conservation Unit, University of Évora, Portugal
[4]Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France
[5]Geobiosphere Science Centre, Department of Physical Geography and Ecosystems Analysis, Lund University, Sweden

Abstract: Potential impacts of projected climate change on biodiversity are often assessed using single-species bioclimatic 'envelope' models. Such models are a special case of species distribution models in which the current geographical distribution of species is related to climatic variables so to enable projections of distributions under future climate change scenarios. This work reviews a number of critical methodological issues that may lead to uncertainty in predictions from bioclimatic modelling. Particular attention is paid to recent developments of bioclimatic modelling that address some of these issues as well as to the topics where more progress needs to be made. Developing and applying bioclimatic models in a informative way requires good understanding of a wide range of methodologies, including the choice of modelling technique, model validation, collinearity, autocorrelation, biased sampling of explanatory variables, scaling and impacts of non-climatic factors. A key challenge for future research is integrating factors such as land cover, direct CO_2 effects, biotic interactions and dispersal mechanisms into species-climate models. We conclude that, although bioclimatic envelope models have a number of important advantages, they need to be applied only when users of models have a thorough understanding of their limitations and uncertainties.

Key words: bioclimatic model, climate change, land cover, model performance, modelling methods, niche properties, scale, species distribution model, species geography, uncertainty, validation.

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*Author for correspondence. Email: risto.heikkinen@ymparisto.fi

I Introduction

Several studies and meta-analyses have indicated that recent climatic change has already affected species' geographical distributions and the persistence of populations (Parmesan, 1996; Walther *et al.*, 2002; Moore, 2003; Parmesan and Yohe, 2003). Furthermore, projected climate changes are likely to have an even greater impact on biota (Berry *et al.*, 2002; Hill *et al.*, 2003; Thomas *et al.*, 2004; Thuiller *et al.*, 2005b). There are many different methodological approaches available for examining the potential effects of climate change on biodiversity, ranging from dynamic ecosystem and biogeochemistry models (eg, Woodward and Beerling, 1997; Peng, 2000) and spatially explicit mechanistic models for single species range shifts (eg, Hill *et al.*, 2001) to physiologically based (eg, Sykes *et al.*, 1996; Walther *et al.*, 2005) and correlative bioclimatic envelope models (eg, Box *et al.*, 1993; Huntley *et al.*, 1995; Iverson and Prasad, 1998; 2001; 2002; Pearson *et al.*, 2002; 2004: Thuiller, 2003; Thuiller *et al.*, 2005b). This paper concentrates on the latter group – statistical bioclimatic envelope models – which are among the most popular approaches to simulate species-climate change impacts.

Statistical bioclimatic modelling techniques aim at defining, for any chosen species, the climate 'envelope' that best describes the limits to its spatial range by correlating the current species distributions with selected climate variables (Beaumont and Hughes, 2002; Berry *et al.*, 2002; Pearson and Dawson, 2003; Thuiller, 2003; Huntley *et al.*, 2004). Assessments of future species' biogeographical ranges are developed by applying the models based on the climate variables that best describe the current equilibrium distributions to simulate future distributions under selected climate change scenarios (Bakkenes *et al.*, 2002; Peterson *et al.*, 2002a; 2002b; 2004; Peterson, 2003; Thuiller, 2003; Pearson *et al.*, 2004; Thomas *et al.*, 2004; Thuiller *et al.*, 2004b; 2005b).

The validity of bioclimatic envelope modelling approaches has been questioned on the grounds that many factors other than climate can significantly influence species distributions and the rate of distribution changes (Hampe, 2004), especially in a simulations of the future. Huntley *et al.* (1989) (see also Huntley, 1998, and references therein) showed that in the Holocene the approach using climate alone did predict distributions even though this distribution included other aspects such as biotic interactions (cf. Davis *et al.*, 1998; Beaumont and Hughes, 2002). In the future, however, extensive habitat fragmentation and species dispersal limitations (Iverson and Prasad, 2002), and impacts of rising atmospheric CO_2 (Woodward and Beerling, 1997; Iverson and Prasad, 2002), soil and fire changes (Brereton *et al.*, 1995; Iverson and Prasad, 1998; Crumpacker *et al.*, 2001) driven by human interactions, genetic differences in populations in different parts of the range, and changing biotic interactions suggest that it is necessary to assess realistically the use of such approaches in future scenarios. Such limitations and uncertainties pose restrictions on bioclimatic envelope models and their results should be interpreted with caution (Pearson and Dawson, 2003; Guisan and Thuiller, 2005).

Nevertheless, bioclimatic envelope models have certain advantages. They offer a tool for undertaking relatively rapid analysis for numerous individual species, and allow the identification of key relationships between species and governing factors of their distributions (Iverson and Prasad, 2001; 2002; Pearson and Dawson, 2003; Gavin and Hu, 2005). They are particularly valuable for providing insight into potential climate warming effects on biodiversity when range-limiting physiological factors for studied species are poorly known (Crumpacker *et al.*, 2001). In addition, individual-species models may provide more precise and realistic predictions than those offered by species-assemblage models (Iverson and Prasad, 1998), not least because species' responses to climate change are thought to be mainly individualistic (Huntley, 1991; Huntley *et al.*, 1995).

However, if we are to develop as accurately as possible bioclimatic envelope models and species range shift scenarios there are a number of critical methodological issues that need to be addressed (Araújo *et al.*, 2005a; Guisan and Thuiller, 2005). Several methodological aspects and decisions in modelling exercises, such as differences between statistical techniques and decisions on which model selection criteria and explanatory variables are used in modelling, can have a notable impact on the accuracy of bioclimatic envelope models, as well as species distribution models in general (Elith *et al.*, 2002; Thuiller *et al.*, 2004b; Guisan and Thuiller, 2005).

Our objectives are to discuss the key methodological issues that may lead to uncertainties in bioclimatic envelope modelling. Based on a review of both earlier and more recent published studies, we assess progress made to improve understanding and reduce uncertainties of predictive bioclimatic modelling. We also highlight issues that appear to be hitherto insufficiently examined in the science of bioclimatic modelling of species distributions. While we acknowledge that there have been an impressive number of bioclimatic modelling studies done, we do not propose to describe them all. Instead, we focus on selected recent developments and studies that are most relevant to the uncertainty issues discussed here.

II Modelling methods and approaches

Statistical bioclimatic envelope models represent one specific type of species distribution models (referred to also as 'habitat models' and 'ecological niche-based models'; see Guisan and Zimmermann, 2000), in which the biogeographical distributions of species are related to broad-scale variation in climate by given modelling techniques (Araújo *et al.*, 2005a; Guisan and Thuiller, 2005). Several techniques have been employed in species distribution modelling in general and in bioclimatic envelope modelling in particular (Franklin, 1995; Guisan and Zimmermann, 2000; Elith and Burgman, 2002; Olden and

Jackson, 2002a; Segurado and Araújo, 2004). A list of approaches used in bioclimatic modelling is provided in Table 1 and these are further discussed below.

Climatic envelope techniques (Environmental envelope techniques) have been used to calculate a fitted, species-specific, minimal rectilinear envelope in a multidimensional climatic space (Boxcar) (Guisan and Zimmermann, 2000). The best-known of these techniques are BIOCLIM (eg, Busby, 1991; Beaumont and Hughes, 2002; Kadmon *et al.*, 2003; Beaumont *et al.*, 2005), the 'Florida Model' (Box *et al.*, 1999), HABITAT (Walker and Cocks, 1991), and DOMAIN (Carpenter *et al.*, 1993). The fuzzy minimal rectilinear envelope modelling applied by Skov and Svenning (2004) also belongs to climatic envelope techniques. Other methods closely related to these techniques have been used by Erasmus *et al.* (2002), Midgley *et al.* (2002) and Miles *et al.* (2004).

BIOCLIM and other environmental envelope techniques, as well as some related methods such as Ecological Niche Factor Analysis (ENFA), are designed to deal with presence-only data (Guisan and Zimmermann, 2000; Kadmon *et al.*, 2003). This is a valuable feature in cases where reliable absence data is not available (Kadmon *et al.*, 2003; Brotons *et al.*, 2004). Paucity of species distribution data is a common situation in remote and poorly inventoried regions. Presence-only models can be useful also for modelling distributions of highly mobile organisms, because valid absences can be difficult to obtain for such species (Guisan and Thuiller, 2005). However, in cases where absence data is available, modelling approaches that employ presence/absence data are generally prioritized and seem to give better predictions (Brotons *et al.*, 2004; Segurado and Araújo, 2004; Pearson *et al.*, 2006).

Classification tree analysis (CTA), also referred to as classification and regression trees (CART), involves rule-based methods that have been used by, for example, Iverson and Prasad (1998; 2001; 2002), Thuiller (2003;

Table 1   Examples of the statistical techniques, and their abbreviations, applied in bioclimatic envelope modelling

Study	Modelling methods
Brereton *et al.*, 1995; Beaumont and Hughes, 2002	BIOCLIM
Kadmon *et al.*, 2003; Meynecke, 2004; Beaumont *et al.*, 2005	
Box *et al.*, 1993; 1999; Crumpacker *et al.*, 2001	'The Florida Model'
Walker and Cocks, 1991	HABITAT
Carpenter *et al.*, 1993	DOMAIN
Baker *et al.*, 2000	CLIMEX
Skov and Svenning, 2004; Svenning and Skov, 2004	Fuzzy minimal rectilinear envelope modelling
Sykes *et al.*, 1996; Walther *et al.*, 2005	STASH
Iverson and Prasad, 1998; 2001; 2002	Classification and regression tree analysis (CTA / CART / RTA)
Guisan and Theurillat, 2000; Price, 2000	Logistic regression/binomial GLM
Bakkenes *et al.*, 2002; Burns *et al.*, 2003	
Leathwick *et al.*, 1996; Midgley *et al.*, 2003	GAM
Araújo *et al.*, 2004; Luoto *et al.*, 2005	
Beerling *et al.*, 1995; Huntley *et al.*, 1995; 2004	Locally weighted regression
Hill *et al.*, 1999; 2002	(local regression/loess)
Berry *et al.*, 2002; Pearson *et al.*, 2002; 2004	ANN
Peterson, 2001; Anderson *et al.*, 2002a; 2002b	GARP
Peterson *et al.*, 2002a; 2002b; 2004	
Prasad and Iverson, 2000	MARS
Gavin and Hu, 2005	GM-SMAP
Thuiller, 2003; 2004; Araújo *et al.*, 2005a; 2005b	GLM, GAM, CTA, ANN
Thuiller *et al.*, 2005a; 2005b	

ANN = artificial neural networks; GAM = generalized additive models; GARP = genetic algorithm for rule-set prediction; GLM = generalized linear models; GM-SMAP = Gaussian mixture distributions and multiscale segmentation; MARS = multivariate adaptive regression splines.

2004), Thuiller *et al.* (2003b) and Araújo *et al.* (2005a; 2005b; 2006). CTA uses recursive partitioning to split the data into increasingly smaller, homogenous, subsets until a termination is reached (Iverson and Prasad, 1998; Venables and Ripley, 2002). The advantage of CTA is that it is allows capturing of non-additive behaviour and complex interactions (De'Ath and Fabricius, 2000; Thuiller *et al.*, 2003b). Moreover, numerical and categorical variables can readily be used together in CTA (Iverson and Prasad, 1998). However, there are limitations in applying CTA. In particular, CTA has a tendency to produce overly complex models that lead to spurious interpretations (Thuiller, 2003; Muñoz and Felicísmo, 2004; Araújo *et al.*, 2005a).

Two closely related parametric approaches, *multiple logistic regression* and *generalized linear models* (GLM) with a binomial distribution and a logistic link, have been employed by Guisan and Theurillat (2000), Price (2000), Bakkenes *et al.* (2002) and Burns *et al.* (2003) (see also Hirzel and Guisan, 2002, and references therein). Using cover-abundance data of plant species, Dirnböck *et al.* (2003) applied a closely related method, ordinal logistic regression models (proportional odds model).

An increasingly popular approach is *generalized additive models* (GAM), which has been used in climate change impact studies by, for example, Leathwick *et al.* (1996), Thuiller (2003; 2004) and Araújo *et al.* (2004). GAMs are non-parametric extensions of GLMs.

They provide a flexible data-driven class of models that permit both linear and complex additive response shapes, as well as the combination of the two within the same model (Bio *et al.*, 2002; Wood and Augustin, 2002). Thus GAMs can cope with regression functions that are of a form not easily approximated by conventional parametric techniques, such as logistic regression (Leathwick *et al.*, 1996). However, possible problems with overdispersion must be handled with caution when fitting GAMs (Leathwick *et al.*, 1996).

Species-climate response surfaces have been developed also using *locally weighted regression* (local regression/loess) (see Cleveland and Devlin, 1988; Venables and Ripley, 2002) by, for example, Huntley *et al.* (1995) and Hill *et al.* (1999; 2002). Local regression is a non-linear flexible method that requires no prior assumption about the form of the relationship between a climate predictor and the species probability of occurrence (Huntley *et al.*, 2004). The method is thus able to capture complex non-linear and multimodal relationships. According to Beerling *et al.* (1995), local regression is also more robust for extrapolation beyond the domain within which the model was calibrated than other modelling methods. A potential disadvantage is that locally weighted regression requires an a priori selection of the bioclimatic predictors to be included in the model (Huntley *et al.*, 2004). A difference between GAMs and local regression is that in the latter method the model is fitted as a single smooth function of all the predictors, whereas in GAMs the effects of the terms in the model are expected to enter the model additively, without interactions between terms (Anonymous, 2001).

Artificial neural networks (ANN) are powerful rule-based modelling techniques which are increasingly used in bioclimatic envelope modelling (eg, Berry *et al.*, 2002; Pearson *et al.*, 2002; Thuiller, 2003; 2004; Araújo *et al.*, 2005a). This method is able to handle explanatory variables from different sources,

such as categorical and boolean data. Moreover, ANN is considered to be robust to 'noise' in the training data set, and it is able to determine climatic envelopes that have non-linear responses to predictors (Hilbert and Ostendorf, 2001; Pearson *et al.*, 2002; 2004). Disadvantages include the requirement of large quantity of data to train, validate and test the network, and the limited insights into the contributions of the predictors in the prediction process (but see Olden and Jackson, 2002b). Moreover, ANN do not allow examining the response curves of species against environmental gradients (Manel *et al.*, 1999; Pearson *et al.*, 2002).

Genetic algorithm for rule-set prediction (GARP) is an artificial intelligence based super-algorithm which uses other techniques (eg, logistic regression, BIOCLIM) in a dynamic machine-learning environment (Stockwell and Peterson, 2002; Anderson *et al.*, 2003). GARP uses species presence records and georeferenced data on ecological factors to produce a model of species' ecological niches. The software is tailored to search for non-random correlations between species presence and absence and environmental characteristics using several different types of rules. GARP works in an iterative process of rule selection, evaluation, testing and incorporation or rejections to produce a heterogeneous rule set summarizing species' ecological requirements (Anderson *et al.*, 2002a). The algorithm can run several thousand iterations. GARP primarily works on presence data points, but it allows for resampling with replacement from the pixels without confirmed presence data in the training set to create a set of pseudo-absence points (Anderson *et al.*, 2003). When projected onto a geographical space, GARP provides predictions of the species' geographical distribution. GARP has been used extensively by A.T. Peterson and collaborators (eg, Peterson, 2001; Anderson *et al.*, 2002a; Peterson *et al.*, 2002b; Stockwell and Peterson, 2002).

Multivariate adaptive regression splines (MARS) is a relatively novel and promising

modelling approach. MARS has been hitherto very rarely applied in either bioclimatic envelope modelling or species distribution modelling in general (but see Prasad and Iverson, 2000; Muñoz and Felicísmo, 2004). This technique combines linear regression, mathematical construction of splines and binary recursive partitioning to produce a local model where relationships between response and predictors are either linear or non-linear.

An extension of MARS is generalized boosted trees or generalized boosted models (GBM) which have been recently introduced in ecology. They are highly efficient in fitting the data, non-parametric and combine the strength of different modern statistical techniques (Ridgeway, 1999; Friedman *et al.*, 2000). Boosting improves predictive accuracies by iteratively estimating classifiers using a base learning algorithm (eg, a decision tree) while systematically varying the training sample. The final boosted classifier's prediction is based upon an accuracy-weighted vote across the estimated classifiers. Recently, boosting has been shown to be a form of additive logistic regression (Friedman *et al.*, 2000), in which the probabilities of class membership can be obtained from boosting. Hitherto, there are very few studies in a context of global change based on generalized boosted models. Clearly, due to the potentiality of this approach such studies might provide important contributions to the climate change modelling.

Two additional novel techniques which have hitherto rarely been applied in geographical species distribution modelling but which also merit further research are maximum entropy method (Maxent) and Random Forests Analysis (or Multiple Tree) (but see Phillips *et al.*, 2006; Prasad *et al.*, 2006). Random Forests generates hundreds or thousands of random trees, evaluates them as a whole and ultimately selects the smallest (most parsimonious) tree that has a given error level (predictive value). Maxent is a machine-learning powerful technique suited particularly for modelling species geographic distributions based on presence-data only. In an extensive comparative study Phillips *et al.* (2006) showed that Maxent was able to perform regularly better (based on AUC measures) in predicting the spatial distribution of two study species than GARP. Moreover, Maxent was more successful in producing detailed (fine-grained) predictions than GARP. Thus this method can provide useful improvements to species-climate change modelling in regions where absence data are not available for species.

III Performance of different modelling techniques

Each of the modelling approaches have their strengths and weaknesses and also differ in their ability to summarize plausible biogeographic responses of species distributions to climatic predictors (Segurado and Araújo, 2004). Moreover, in assessments of the potential impacts of climate change, seemingly small differences in the accuracy of models in predicting current distributions may result in disturbingly dissimilar projections of future distributions (Thuiller, 2003; 2004).

1 Measures of prediction accuracy
One criterion for evaluating performance of models is to measure the accuracy of the predictions (ie, prediction error; see Fielding, 2002), preferably based on independent data sets. There are several measures that can be used in evaluating the classification accuracy of the presence/absence models (Fielding and Bell, 1997; Pearce and Ferrier, 2000a). However, currently the discrimination ability of the species distribution models is mainly assessed using two measures: the Kappa statistic (Cohen's Kappa) (Congalton, 1991), and the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding and Bell, 1997).

The Kappa coefficient measures the correct classification rate (proportion of correctly classified presences and absences) after the probability of chance agreement has been removed (Congalton, 1991). Landis and Koch (1977)

proposed a scale to describe the degree of concordance based on Kappa: 0.81–1.00 = almost perfect; 0.61–0.80 = substantial; 0.41–0.60 = moderate; 00.21–0.40 = fair; 0.00–0.20 = fail. Kappa is dependent on a single threshold to distinguish between predicted presence and predicted absence and thus falls into the class of threshold-dependent measures. The earlier practice of using a 0.5 cut-off probability as a rule of thumb has shown to be inadequate (Manel *et al.*, 2001; Segurado and Araújo, 2004; Liu *et al.*, 2005). A more objective and increasingly popular approach is to select an optimum probability threshold based on the cut-off level that maximizes Kappa. This can be determined by evaluating Kappa values at successive probability increments across the entire range from 0.00 to 1.00 (Huntley *et al.*, 2004).

A recent important evaluation of the approaches to select an optimal threshold for transforming the species distribution predictions to presences/absences was provided by Liu *et al.* (2005). The authors compared 12 approaches for selecting the threshold of occurrence. Their results challenged the commonly used kappa maximization approach because it was not among the most robust methods. Instead, the threshold-determining approaches recommended by Liu *et al.* (2005) included (i) prevalence (ie, the number of occurrences in relation to the number of samples) approach (taking the prevalence of model-building data as the threshold); (ii) average probability/suitability approach (taking the average predicted probability/suitability (ie, the mean value of predicted probabilities of species presence) of the model-building data as the threshold); and (iii) using data sets with prevalence of 50% to build models.

An alternative measure of accuracy is the AUC of the ROC plot. AUC relates relative proportions of correctly classified (true positive proportion) and incorrectly classified (false positive proportion) cells over a wide and continuous range of threshold levels (Cumming, 2000; Erasmus *et al.*, 2002). This makes it a threshold–independent measure (Pearce and Ferrier, 2000a). The AUC ranges generally from 0.5 for models with no discrimination ability to 1.0 for models with perfect discrimination. An approximate guide for classifying the accuracy of AUC is that proposed by Swets (1988): 0.90–1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; 0.50–0.60 = fail. AUC values of less than 0.5 indicate that the model tends to predict presence at sites at which the species is, in fact, absent (Elith and Burgman, 2002).

2 Comparisons of modelling techniques

Bioclimatic envelope modelling studies have usually been conducted by employing only one modelling approach (eg, Box *et al.*, 1993; Huntley, 1995; Iverson and Prasad, 1998; 2001; Bakkenes *et al.*, 2002; Beaumont and Hughes, 2002; Berry *et al.*, 2002; Pearson *et al.*, 2002; 2004; Huntley *et al.*, 2004; Beaumont *et al.*, 2005), or different variations of the same technique, eg, GARP (Anderson *et al.*, 2002a; 2003; Peterson, 2003). Some variation is expected from using different techniques because different models use a variety of assumptions, algorithms and parameterizations. Thus, when studies use a single modelling technique there is no information of whether the selected method provides the best predictive accuracy for the particular data set used (Araújo and New, 2006).

A number of comparative studies have examined the performance of different species distribution modelling techniques (Franklin, 1995; Manel *et al.*, 1999; Bio *et al.*, 2002; Elith and Burgman, 2002; Moisen and Frescino, 2002; Olden and Jackson, 2002a; Thuiller *et al.*, 2003a; Muñoz and Felicísmo, 2004; Segurado and Araújo, 2004), although in the context of climate change such appraisals are rare (but see Thuiller, 2003; 2004; Araújo *et al.*, 2005a; Pearson *et al.*, 2006).

When assessing model variability in the context of present-time bioclimatic modelling,

some studies have reported only subtle differences among techniques. For example, Franklin (1995) reported that GAM, GLM and CTA produced all projections with similar accuracy. In contrast, using the same three methods and data on plant species at three different scales, Thuiller *et al.* (2003a) showed that CTA had a lower overall model performance than the two generalized methods. In a study by Bio *et al.* (2002) more than half of the species were better modelled by GAM than by GLM, indicating that species' responses are often complex and difficult to fit using simple symmetric response shapes. Elith and Burgman (2002) reported an apparent trend towards better model discriminatory performance from GAM and GLM in comparison to ANUCLIM (climatic envelope method) and GARP. The authors stated that GARP appears to perform better than the other three methods when tested with original data, but testing with independent data indicated no clear differences in the accuracy of models. These results seem to contradict the optimistic statements of Peterson and Cohoon (1999) and Anderson *et al.* (2003), who have suggested that GARP is especially successful in predicting species' distributions under a wide variety of situations. Also the results of Pearson *et al.* (2006) indicate that GARP may yield projections that markedly differ from theoretically more robust semi-parametric techniques.

Contrasting results have also been obtained using ANN. Olden and Jackson (2002a) stated that, on average, ANN outperformed logistic regression, linear discriminant analysis and CTA, although all approaches predicted species presence/absence with moderate to excellent success (cf. Thuiller, 2003; Araújo *et al.*, 2005a). In an extensive evaluation study with seven modelling methods, Segurado and Araújo (2004) concluded that ANN performed generally best, immediately followed by GAMs including a covariate term for spatial autocorrelation. In contrast, Manel *et al.* (1999) concluded that ANN do not currently have major advantages over logistic regression

and discriminant analysis as regards model performance. However, it is important to note that ANN, as well as other modelling techniques, are sensitive to small variations in model parameterization. Unless studies equal parameterizations for a given technique, results from models are not entirely comparable (Segurado and Araújo, 2004). Multivariate adaptive regression splines (MARS) has rarely been included in comparative studies. However, it has been shown to perform in several cases better than CTA, ANN or logistic regression (Moisen and Frescino, 2002; Muñoz and Felicísmo, 2004).

Comparisons of modelling techniques in the context of climate change are more recent and provide evidence of previously unnoticed levels of variability across modelling techniques (Thuiller, 2003; 2004; Araújo *et al.*, 2005a; 2005b; Pearson *et al.*, 2006). For example, in Thuiller (2003) CTA appeared as the weakest method with a tendency to overfit. ANN performed slightly better than the other methods but showed also a tendency to overfit during the calibration process. GAM and GLM did not appear to overfit and had a higher accuracy than ANN in several cases. The results of the follow-up study by Thuiller (2004) indicated that the variability across model projections of species future ranges from GLM, GAM, ANN, and CTA can be large and even override the variability arising from the use of a range of climate change scenarios.

In a bioclimatic modelling study based on 116 breeding bird species in Britain at two time periods (Araújo *et al.*, 2005b), models yielded projections that were variable both in magnitude and direction. For example, 90% of the species were projected both to expand and to contract depending on the modelling technique and calibration used. Araújo *et al.* (2006) examined projected potential distributions of European amphibian and reptile species under a set of climate change scenarios. As with the UK birds study, they detected considerable amount of methodological uncertainty as model projections were

extremely variable. Pearson *et al.* (2006) applied nine modelling techniques to model current and potential future distributions of four target species in South Africa. Their results showed significant differences between predictions from different models, with predicted changes in range size by 2030 differing in both magnitude and directions.

Some general conclusions can be drawn from these comparative studies. First, the best model performance has been most often attributed to techniques using complex approaches to mode fitting; GAM, ANN, and recently also MARS (but see Elith *et al.*, 2006; Lawler *et al.*, 2006). These methods thus represent perhaps the most reliable choices for bioclimatic modelling exercises employing only one modelling method. However, it should be noted that some of the techniques, eg, GARP and locally weighted regression, have rarely been included in comparative studies (but see Elith and Burgman, 2002; Pearson *et al.*, 2006). Moreover, under certain circumstances (for example interpolations made within a given region and time period) most of the methods are able to provide moderate or excellent performance.

3 Approaches to account for model predictions' variability

As a response to the variability in the model performance between different methods, two recent developments to reduce the uncertainty in species-climate impacts modelling have been defined (Araújo and New, 2006). Rather than using a single modelling technique investigators can (i) use a framework including different methods and models for each species and select the most accurate technique using both evaluation methods and expert knowledge (Thuiller, 2003; 2004), or (ii) use majority vote criterion approach among multiple models thus deriving a single projection that represents the central tendency across all models considered. Thuiller (2004) used a consensus analysis based on principal components analysis (PCA) to derive composite variables that summarize

the highest amount of information from individual projections from different methods (GLM, GAM, CTA, ANN) (see also Anderson *et al.*, 2003; Thuiller *et al.*, 2005b). This approach was further explored and its usefulness demonstrated in a study by Araújo *et al.* (2005b) where the authors were able to test the results of bioclimatic models applied to bird distributions in Great Britain using two data sets in different time periods subject to climate change. The results of models were found to be extremely variable across species and modelling methods. Using a consensus approach authors were able to produce forecasts with significantly reduced uncertainties. However, as pointed out by Araújo *et al.* (2005b), averaging the model projections will mainly increase the accuracy of forecasts when better models (eg, models based on techniques that generally provide superior overall performance and perform consistently well across a range of species) and not merely more models are taken into account. Improved accuracy will thus also critically depend on traditional challenges of trying to build better models with improved data. However, there is a possibility that models providing realistic projections are a minority within one ensemble of forecasts. Thus they would contribute little to building a consensus among an ensemble of forecasts. An alternative for combining forecasts is proposed by Araújo *et al.* (2006), whereby different clusters of model projections are produced and consensus is calculated within each cluster. This allows simple conditional statements of probabilities to be made, whereas the full breadth of variability provided by an ensemble of forecasts is still preserved (for extended discussion see Araújo and New, 2006).

IV Model validation approaches and bioclimatic envelope models

A wealth of literature is available on the evaluation, validation and confirmation of numeric models (Oreskes *et al.*, 1994; Harrell *et al.*, 1996; Rykiel, 1996; Fielding and Bell, 1997; Guisan and Zimmermann, 2000;

Araújo *et al.*, 2005a). However, the perspectives presented have varied considerably. Oreskes *et al.* (1994) takes an extreme view that because all natural systems are not closed model results are always non-unique, and verification or validation of numerical models is impossible. These authors argued that the primary value of models is heuristic and that predictions will always be open to question. Others have provided less extreme standpoints. For example, Harrell *et al.* (1996), Fielding and Bell (1997) and Olden *et al.* (2002) contend with discussing the following strategies for model validation: resubstitution (no partitioning is carried out, the data used to calibrate models are also used to validate them); bootstrapping and leave-one-out jack-knifing; (one-time) data splitting; grouped cross-validation (also known as *k*-fold partitioning, hold-out, or external method).

A recent contribution to the debate of model validation under climate change was provided by Araújo *et al.* (2005a). The authors argued that the validation of species-climate envelope models has been insufficiently explored and this has contributed to creating an optimistic perception of their true performance in climate-change impact assessments. This is not surprising since validation of models is often made with non-independent data as predictions concern events that have not yet occurred. In some cases species range shift projections (eg, Sætersdal *et al.*, 1998; Beaumont and Hughes, 2002) were made without attempts to validate the predictive accuracy of models being presented. However, most bioclimatic envelope modelling studies (eg, Brereton *et al.*, 1995; Huntley *et al.*, 1995; Bakkenes *et al.*, 2002; Midgley *et al.*, 2002; Huntley *et al.*, 2004; Skov and Svenning, 2004) have used the resubstitution approach, ie, using the same data for training and testing (Figure 1a). Resubstitution is currently not considered a desirable option, because it tends to give optimistically biased estimates or error rates and model performance (Harrell *et al.*, 1996; Fielding and Bell, 1997; Olden *et al.*,
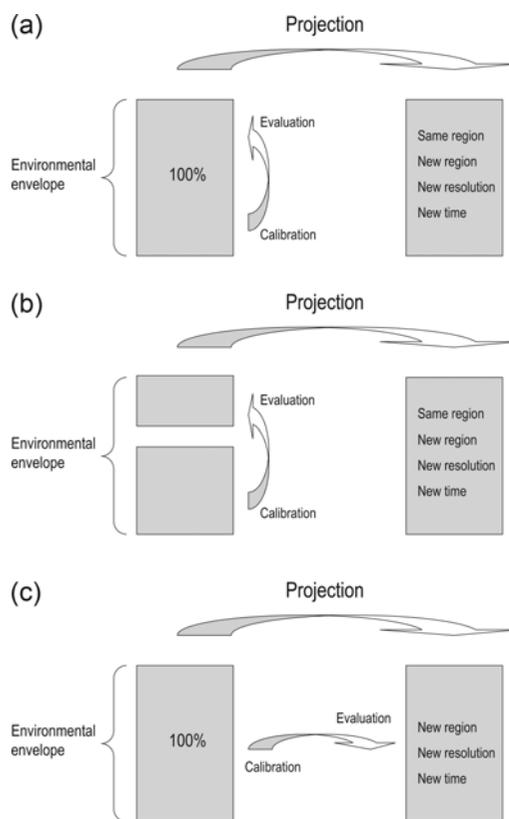

Figure 1 Three main approaches for calibrating and validating species-climate envelope models: (a) resubstitution; (b) one-time data splitting (split-sample approach); and (c) independent validation
Source: Reprinted from Araújo *et al.* (2005a).

2002; Thuiller, 2003; Muñoz and Felicísmo, 2004; Thuiller, 2004).

Data partitioning approaches in model validation have increasingly been applied to circumvent the problems of resubstitution approach. The most commonly used approach is one-time data splitting (ie, split sample; see Harrell *et al.*, 1996; Guisan and Zimmermann, 2000), whereby data is randomly split into calibration and validation subsets (Figure 1b). This approach has been used

in bioclimatic envelope modelling by Box *et al.* (1993), Iverson and Prasad (1998), Berry *et al.* (2002), Pearson *et al.* (2002; 2004), Thuiller (2003; 2004), Araujo *et al.* (2004), among others (for review, see Araújo *et al.*, 2005a).

Some of the studies have used bootstrap method (Peterson *et al.*, 2002a; 2004; Peterson, 2003) or fourfold cross-validation (Luoto *et al.*, 2006a). However, as with data splitting, bootstrapping and cross-validation take samples randomly from the original data. Although they provide a more robust measure of model performance than resubstitution, they may also provide non-independent samples that are vulnerable to certain pitfalls of correlative models based on geographical data, especially spatial autocorrelation. Spatial autocorrelation may bias the accuracy of models that are fitted with samples from the original data even when these are obtained with additional field sampling within the modelled region (Vaughan and Ormerod, 2003; Araújo *et al.*, 2005a).

The best option to validate bioclimatic envelope models is to use independent test data collected from another region (eg, Beerling *et al.*, 1995; Price, 2000; Randin *et al.*, 2006) or from another point of time (Araújo *et al.*, 2005a; Araújo and Rahbek, 2006; see Figure 1c). One of the most important challenges in bioclimatic modelling is to understand the limitations of models by calibrating and validating models with data that are distinctively independent from each other. This is because predicting species distribution patterns at one point of time distant from that used to calibrate the models is one of the chief purposes of bioclimatic envelope models. To date, such studies have been very rare (but see Hill *et al.*, 1999; Araújo *et al.*, 2005a; 2005b; Walther *et al.*, 2005).

The results of Araújo *et al.* (2005a) showed that accuracies of correlative bioclimatic envelope models for 116 UK birds were always higher when evaluated by one-time split sample than accuracy values derived from fitting the calibrated model to the independent data recorded *c*. 15 years later than the calibration data. This result supported concerns that models' predictive accuracy measured by one-time data splitting (and other related validation methods) are likely to provide generally overoptimistic assessment of model performance on truly independent data. In contrast, using a physiologically based climatic envelope model (STASH), Walther *et al.* (2005) compared detailed past climatic and distribution records of *Ilex aquifolium* with the current climate and distribution. In this case the model predicted well the new suitable areas available for the species to be colonized. The authors concluded that a shift in the northern margin of *Ilex aquifolium*, in concert with increasing winter temperatures, was demonstrated.

V Uncertainty issues in model building

There are several decisions which may contribute to uncertainty in the models and should thus be taken into account when developing species distribution models (including bioclimatic envelope models) (Elith *et al.*, 2002). Sources of uncertainty in models have received a considerable attention in the statistical and ecological literature (Chatfield, 1995; Harrell *et al.*, 1996; Buckland *et al.*, 1997; Guisan and Zimmermann, 2000; Vaughan and Ormerod, 2003; Johnston and Omland, 2004; Rushton *et al.*, 2004). This attention is warranted because there is increasing evidence that the 'best' model developed for a given studied region is only one among many alternative models.

Research has been primarily concerned with regression models (GLM, GAM). However, many of the methodological uncertainties discussed for these techniques apply to other approaches (Vaughan and Ormerod, 2003). Factors contributing to the uncertainty of model projections include, for example, decisions associated with model building (a priori selected predictors versus manual selection versus automated model selection), collinearity, choice of the variable and model selection criteria, identifying and excluding outliers, autocorrelation and overdispersion,

and finding a balance between underfitted ('overly parsimonious') and overfitted (over-parametrized) models (Nicholls, 1989; Crawley, 1993; Chatfield, 1995; Mac Nally, 2000; Elith *et al.*, 2002; Heikkinen *et al.*, 2004; Johnston and Omland, 2004).

1 Model building approaches
Basically, there are three approaches to develop a single final model in a multiple regression setting: (i) a priori selection of a set of explanatory variables, (ii) manual model building, and (iii) automated model calibration. Automated model building is a commonly available option in the majority of statistical packages (eg, S-Plus, SPSS). It is also embedded in some novel modelling frameworks such as GRASP (Lehmann *et al.*, 2003) and BIOMOD (Thuiller, 2003). The strong point of this approach is that several hundreds of species can be analysed and their potential range shifts examined within one computer run in a reasonable amount of time. Moreover, BIOMOD framework can run analysis for each species using several different modelling techniques or different forms and parameterizations of one particular method (Thuiller, 2003).

A disadvantage of the automated model selection approach is that critical steps and alternative pathways in model building are not as transparent and controlled as in manually conducted modelling exercises. Automated selection of variables may thus result into biologically implausible models and selection of irrelevant (or noise) variables (James and McCulloch, 1990; Pearce and Ferrier, 2000b). Particularly, when modelling a limited set of indicator species vulnerable to climate change, manual model building may provide an appropriate, 'hands-on' process that gives a better control to the modeller than automated techniques and enables the development of ecologically plausible models (Nicholls, 1989; Crawley, 1993; Pausas *et al.*, 2003). As highlighted by Leathwick *et al.* (1996), increasing sophistication in analytical tools is no substitute for specific and detailed

insight into the behaviour of complex ecological systems. Chatfield (1995) referred to model building as a process involving formulating, fitting and checking a model in an iterative and interactive way. However, when dealing with several hundreds of species this approach can be time-consuming and difficult to apply. Moreover, both with manual and automated model building the modeller needs to pay attention to other sources of uncertainty, such as collinearity and overfitting.

The third option, a priori selection of a limited number of predictors in the models, has been used in a number of bioclimatic modelling studies (eg, Beerling *et al.*, 1995; Sykes *et al.*, 1996; Hill *et al.*, 2002; Huntley *et al.*, 2004). A disadvantage of this approach is that it requires an a priori decision as to the selection of bioclimatic variables to be included in the model. However, when empirical information about the physiological limits constraining species' geographical distributions are available, a priori selection of appropriate predictor variables may well turn into an advantage (Huntley *et al.*, 2004). Moreover, by using a limited number of physiologically meaningful variables the modeller may more readily circumvent the potential collinearity and overfitting problems (cf. Mac Nally, 2000; Beaumont and Hughes, 2002; Beaumont *et al.*, 2005). A possible shortcoming is that, when models are applied to new regions, the studied species may respond to the a priori selected variables differently. For example, species may show a strong correlation with a particular predictor variable in one area and little response in another area (Osborne and Suárez-Seoane, 2002; Pearson and Dawson, 2003). Also it is possible that presence or absence of a given species is highly correlated with climatic variables excluded from the a priori selected set. This may happen because of the correlations between the predictor variables (Beerling *et al.*, 1995) or because a particular response is observed only in certain parts of the study area (see Osborne and Suárez-Seoane, 2002, and references therein).

2 Overfitting and model selection criteria

One of the crucial issues in species distribution modelling is the identification of the optimal trade-off between producing underfitted and overfitted models, and developing an understanding of the factors that may result into these two phenomena (Harrell *et al.*, 1996; Elith *et al.*, 2002; Vaughan and Ormerod, 2003). Some studies include what seems to be an exceeded number of climatic variables and are thus vulnerable to unbalanced observations per predictors ratio, as well as to potential overfitting problems (see Brereton *et al.*, 1995; Beaumont *et al.*, 2005; Guisan and Thuiller, 2005). Briefly, this means that overfitted models including too many explanatory variables are exceedingly complex and may begin to fit random noise in the data (Chatfield, 1995; Fielding, 2002). Although more complicated models may appear to give a better fit, the predictions they produce may be poorer (Chatfield, 1995). The study by Beaumont *et al.* (2005) suggests that the use of BIOCLIM with all its 35 climatic variables may lead to overfitting and therefore affect the potential usefulness of projections. The authors also showed that the size of the predicted species' distributions using all 35 variables were on average half of the size of the distributions produced using only six relevant parameters.

Certain modelling techniques (particularly CTA) have a higher tendency to overfitting than others (Thuiller, 2003; Araújo *et al.*, 2005a). However, many factors other than the choice of the technique can have an impact on the number of predictors selected in the final models. One of these factors includes the model selection criteria. A 'traditional' model selection approach in regression modelling is selecting significant predictors using forward or backward (or both) stepwise procedures. The decision as to whether a variable is included or dropped from the model can be judged by F-statistic or χ^2 statistic (Crawley, 1993; Lehmann *et al.*, 2003; Johnston and Omland, 2004).

Recently, there has been a trend towards using Bayesian information criterion (BIC) (also known as Schwarz criterion) or Akaike's information criterion (AIC) in model selection (Rushton *et al.*, 2004). AIC has two components: negative log-likelihood, which measures lack of model fit to the observed data, and a bias correction factor, which increases as a function of the number of model parameters (Johnston and Omland, 2004). AIC is equivalent to twice the log-likelihood of the model fitted plus two times the number of parameters included in the model (Rushton *et al.*, 2004).

BIC is superficially similar to AIC and has also two components: negative log-likelihood, and a penalty term that varies as a function of sample size (increases as sample size increases) and the total number of parameters (Johnston and Omland, 2004). Advantages of AIC and BIC include the fact that they can be used to make inferences from more than one model and they consider both model fit and complexity simultaneously. Applying different model selection approaches to the same data may result in differently parameterized models. Thus, the choice of model selection criterion is important and is likely to affect the accuracy of predictions. Bio *et al.* (2002) considered that BIC leads into more reliable and parsimonious (simpler) models (see also Buckland *et al.*, 1997). Sometimes BIC may lead to too strict (underfitted) models that do not capture some of the important relationships between response and predictor variables (Bio *et al.*, 2002). According to Johnston and Omland (2004) AIC is a generally favoured option. However, the consequences of choosing among the AIC, BIC or 'traditional' F- and χ^2 statistics in model selection has been poorly examined and it remains a field with a need for further inquiry.

Recent work by Maggini *et al.* (2006) has further challenged the model selection approaches by reporting that two alternative approaches that are currently available in GRASP, cross-selection and the Bruto method (Venables and Ripley, 2002: 234), appear to have clear advantages over AIC,

BIC or *F*-statistics. They concluded that, while AIC appears to be very conservative and BIC too selective, cross-selection creates more stable models (based on ROC statistics) and the Bruto method has the advantage of providing automatic selection of smoothing degrees of freedom and increasing computational speed.

3 Sample size

The sample size also affects model selection and the predictive performance of the model (Cumming, 2000; Peterson *et al.*, 2002a; Araújo *et al.*, 2005b). Stockwell and Peterson (2002) studied the effects of sample size on the accuracy of species distribution models using GARP, logistic regression, and a surrogate method with a single environmental variable. Their results suggest that machine-learning methods such as GARP can reach a near maximal average success at predicting species' occurrences with 50 data points, whereas the remaining two methods reached their maximum accuracy at *c*. 100 data points. This indicates that species distribution models based on fewer data points than 100 may provide less robust models.

However, the assumption that a sample of 100 data points provides a maximum potential predictive accuracy of models in all situations is probably too optimistic. Pearce and Ferrier (2000b) showed that in their data a clear increase in the discrimination performance of the models was observed between the 250 and 500 sample sizes. The results of McPherson *et al.* (2004) suggested that optimal models had large sample sizes, in their case between 300 and 500 (see also Cumming, 2000; Reese *et al.*, 2005). Araújo *et al.* (2005a) demonstrated that using a 70% random sample instead of the total 2861 10-km grid squares reduced the predictive performance of British bird models dramatically.

These results indicate that the more data are available for model building the better. However, increasing the sample size may also produce some undesirable effects. This is because the relatively high sample size tends to lower p-values compared to smaller sample sizes (McBride *et al.*, 1993). When data consists of several thousands data points (which is not unfamiliar with atlas data sets) it is easy to obtain statistically significant differences, even though the predictors account for only a minor part of the variation in the species distribution data (cf. Crawley, 1993: 57). It is thus advisable to be cautious when building models with large data sets in order to avoid overparameterized models that include variables with little ecological relevance. When model selection is based on stepwise procedures using F-statistics or χ^2 statistics, this can be done by applying a more stringent *p*-value as the variable selection criteria than the commonly used 0.05. However, as regards AIC and BIC, very little research has been carried out of their behaviour to varying sample sizes. In the future, new work should be addressed to assess relationships between sample size and different model selection criteria so as to understand their synenergetic impacts on the accuracy of species-climate models.

VI Multicollinearity and autocorrelation

1 Multicollinearity

Multicollinearity among predictors may hamper the analysis of species-environment relationships in multiple regression settings. Due to collinearity, ecologically more causal variables may be excluded from the models if other intercorrelated variables explain the variation in response variable better in statistical terms (Mac Nally, 2000; Luoto *et al.*, 2002; Heikkinen *et al.*, 2004). However, in bioclimatic modelling studies very little attention has hitherto been paid to multicollinearity (Guisan and Thuiller, 2005; Luoto *et al.*, 2006a). Future contributions would be required to amplify our better understanding of the possible biases in species-climate modelling arising from collinearity problems.

Approaches to tackle collinearity include the examination of the correlation or variation

inflation factors (VIFs) between the predictors, and dropping some of the highly inter-correlated variables from the analysis (Cawsey *et al.*, 2002; Elith and Burgman, 2002) (but see Philippi, 1993). Data-reduction techniques have also been applied, such as using principal components analysis (PCA) to reduce the dimensionality of the predictor data set (Gates and Donald, 2000; Suárez-Seoane *et al.*, 2002; Muñoz and Felicísmo, 2004). However, one disadvantage of using PCA is the difficult interpretation of its outputs. Furthermore, some variables that are irrelevant to a species' distribution may contribute to the principal components (Gates and Donald, 2000; Vaughan and Ormerod, 2003), creating a false expectation of their relevance for species distribution modelling.

Recent developments have provided alternative means of addressing collinearity within species distribution models. When aiming at prediction with regression analysis, valuable insights can be developed by sequential regression and structural equation modelling (Graham, 2003). Collinearity can also be addressed by variation partitioning (Borcard *et al.*, 1992) and hierarchical partitioning methods (Chevan and Sutherland, 1991; Mac Nally, 2000), which are designed to provide more in depth understanding of the explanatory powers of predictors (Watson and Peterson, 1999). These methods provide a dissection of the variation in response variable(s) into independent components which reflect the relative importance of individual predictors or groups of predictors and their joint effects (Anderson and Gribble, 1998; Cushman and McGarigal, 2004; Heikkinen *et al.*, 2004; 2005). In a recent work, Gibson *et al.* (2004) provided a useful approach to species distribution modelling by combining logistic regression, model selection based on AIC and hierarchical partitioning into the same modelling framework. Hierarchical partitioning was used to support the identification of predictor variables most likely to influence the variation in the target-species distribution.

2 Spatial autocorrelation

Autocorrelation is a frequently observed feature in spatially sampled biogeographical data (Diniz-Filho *et al.*, 2003), which can hamper attempts to identify plausible relationships between species distributions and explanatory variables (Legendre, 1993; Segurado *et al.*, 2006). Due to spatial autocorrelation, values of particular variables in neighbouring sites are more or less similar than they would be in a random set of observations (Legendre, 1993).

Recent biogeographical studies have increasingly addressed spatial autocorrelation in broad-scale biodiversity modelling (eg, Selmi and Boulinier, 2001; Lichstein *et al.*, 2002; Diniz-Filho *et al.*, 2003; Diniz-Filho and Bini, 2005; Ferrer-Castán and Vetaas, 2005). There are several different approaches to explore spatial structure in the data, including: (i) applying generalized least squares (GLS), where spatial correlation structure is incorporated assuming exponential, spherical or Gaussian relationships between error terms and geographical distances (Selmi and Boulinier, 2001; Diniz-Filho and Bini, 2005); (ii) using geographical coordinates of the sampled data points and their higher and cross-product terms in the modelling exercise (trend-surface analysis) and associated variation partitioning analysis (eg, Heikkinen and Birks, 1996; Lichstein *et al.*, 2002; Titeux *et al.*, 2004; Ferrer-Castán and Vetaas, 2005); and (iii) comparing semivariograms or Moran's *I* coefficients of the field data and of the model residuals to see how much of the spatial autocorrelation structure in the species data is accounted for by the environmental variables (Bio *et al.*, 2002; Hawkins *et al.*, 2003). According to Diniz-Filho *et al.* (2003) and Ferrer-Castán and Vetaas (2005), strong correspondence between the spatial structures of both species data and environmental data may increase the danger that accounting statistically for spatial component (eg, by partial regression or spatial GLS) downplays the significance of environmental variables.

A recent novel approach to use eigenvector-based spatial filters that are capable to capture spatial structures at different scales (Borcard and Legendre, 2002; Griffiths, 2003; Borcard *et al.*, 2004; Diniz-Filho and Bini, 2005). These filters can be used as predictors in (partial) multiple regression analysis to take the spatial autocorrelation into account as effectively as possible (Diniz-Filho and Bini, 2005).

However, these recent developments in accounting for spatial autocorrelation has predominantly concerned species richness modelling. As regards species distribution modelling and particularly bioclimatic envelope modelling, progress has been more modest (but see Araújo *et al.*, 2005a; Segurado *et al.*, 2006). In species-environment modelling one of the approaches to account for the patch-like autocorrelation in the data is to use autologistic models in which information of the response variable from the neighboring sampling points is used to produce a summary (autocovariate) variable (Augustin *et al.*, 1996; Heikkinen *et al.*, 2004). Another option is to use spatial autoregressive models in which a spatial autocorrelation (SCA) term is added to the linear predictor to reduce the spatial structure in the model residuals (Lichstein *et al.*, 2002; Guisan and Thuiller, 2005).

Overall, there is a need for additional studies assessing the importance of autocorrelation within bioclimatic modelling and more importantly to investigate approaches to circumvent or deal with the issue. This is because species-climate studies are often based on atlas data sets that are most likely vulnerable to autocorrelation (Diniz-Filho and Bini, 2005). However, integrating spatial autocorrelation effects into bioclimatic modelling in a context of global change can be problematic. More specifically, it is unlikely that spatial structure described under current conditions will be maintained in the future because they indirectly reflect the effects of historical, dispersal and environmental factors (Guisan and Thuiller, 2005).

VII Species geographical and ecological characteristics and performance of species-climate models

By definition, bioclimatic envelope models examine the relationship between climatic variables and species distributions. However, there is evidence that the performance of species-climate models may be influenced by the characteristics of the species distribution patterns. Stockwell and Peterson (2002) noted that predictive accuracy of GARP was not independent of range size; widespread species were modelled less accurately. Similar results had been discussed by Araújo and Williams (2000), using logistic regression. Fielding and Bell (1997), Manel *et al.* (2001) and McPherson *et al.* (2004) argued that species prevalence can also have an impact on the accuracy of the species distribution models, measured either by Cohen's kappa or AUC. However, the results of these papers were not fully coincident. According to Manel *et al.* (2001) kappa was only marginally affected by prevalence and AUC values were wholly independent of it. In contrast, McPherson *et al.* (2004) argued that kappa is sensitive to variation in prevalence values and AUC provides a more reliable measure of model performance. McPherson *et al.* (2004) concluded that models perform best when prevalence is intermediate (see also Virkkala *et al.*, 2005).

Other species spatial characteristics might also affect model performance (Brotons *et al.*, 2004; Segurado and Araújo, 2004; Luoto *et al.*, 2005). In a simulation experiment, Reese *et al.* (2005) showed that model accuracy was positively related to the level of contiguity in the distribution maps. This suggests that species with high spatial contiguity might be better modelled than species with low contiguity. Brotons *et al.* (2004) reported that the predictive accuracy of the models was generally higher for more marginal species (marginality = distance of species' mean distribution in environmental space relation to the global mean). In a comprehensive modelling study, Segurado and Araújo (2004) investigated the

effects of two species geographical character-
istics (area of occupancy and extent of occu-
pancy) and two species-environmental
characteristics (marginality and niche breath)
on models' accuracy. Their results indicate a
clear trend towards increasing model perform-
ance for restricted-range species and decreas-
ing performance for widespread species.
Segurado and Araújo (2004) also noted that
model performance is higher for species with
high environmental marginality and low niche
breath than for generalist species.

   Three recent studies have also demon-
strated the sensitivity of model projections for
the geographical distribution and ecological
properties of the target species (Kadmon
et al., 2003; Luoto *et al.*, 2005; Thuiller *et al.*,
2005a). Kadmon *et al.* (2003) showed that
species characterized by high prevalence
within a limited range of climatic conditions
were modelled with higher precision than
rarer ones with wide climatic ranges; thus,
niche breath had a negative effect on model
accuracy. The results of Luoto *et al.* (2005)
suggested that the performance of species-
climate models for boreal butterflies
were negatively correlated with latitudinal
range (geographical extent of distribution)
and prevalence, and positively with spatial
autocorrelation (clumping of distribution)
(Figure 2). In other words, species at the mar-
gin of their range or with low prevalence were
better predicted than widespread species, and
species with clumped distributions better
than widely scattered dispersed species. The
overall message emerging from these studies,
as well as other recent studies discussed here,
is that species geographical attributes can sig-
nificantly influence the behaviour and uncer-
tainty of pure species-climate models, which
should be taken into account in assessments
of climate change impacts.

VIII Sampling and delineating climatic predictors and equilibrium of species' distributions with climate

An accurate description of species-environment
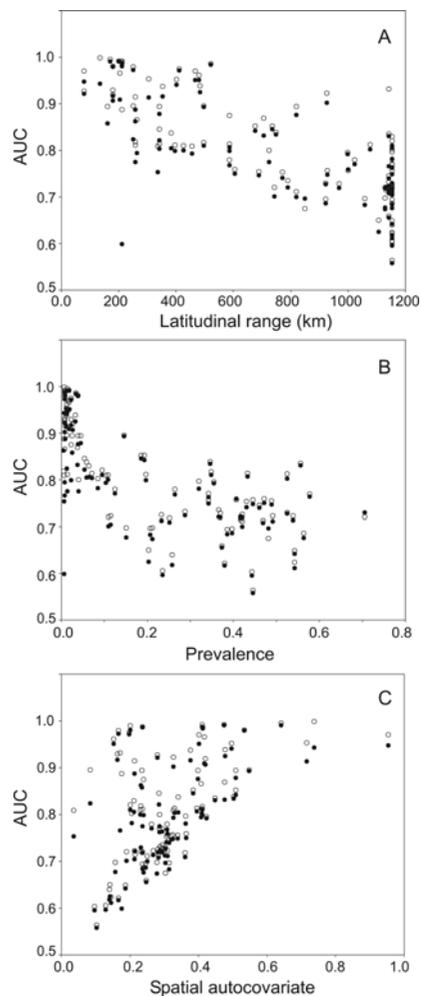relationships requires that samples are taken

Figure 2 The effects of (A) latitudinal
range (geographical extent of
distribution); (B) prevalence; and (C)
clumping of distribution (measured as
spatial autocorrelation) on the accuracy
of species-climate models for the
distributions of 98 butterfly species in
Finland. Accuracy of models was
measured by area under curve (AUC)
values from the ROC plots. Results are
shown both as resubstitution (open
symbols) and cross-validation (solid
symbols) statistics
Source: Reprinted from Luoto *et al.*
(2005).

across the complete gradient of environmental space in which species occur. Such sampling should include sites defining the boundaries of species environmental distributions (Vaughan and Ormerod, 2003). Kadmon *et al.* (2003) reported that the climatic bias in sampling can have a significant effect on the accuracy of model predictions and reduce model performance. Thuiller *et al.* (2004c) examined the consequences of restricting the range of environmental conditions over which species-climate models are developed. The authors showed that the incomplete sampling of the climatic range can strongly influence the estimation of response curves, especially towards upper and lower ends of environmental ranges (see also Pearson *et al.*, 2006). This may reduce the applicability of the models for predictive purposes and produce spurious projections of species' distributions into the future. In conclusion, projections of species' future distributions should be evaluated carefully if the model calibration data is not covering the full range of environmental gradients which species inhabit.

Incomplete coverage of projected *future* climates can also produce prediction errors. For example, in the Northern Hemisphere species are generally projected to move northwards. In many studies, southernmost regions are projected to experience a future climate that has no modern analogue in the study region. In such cases modelling results provide incomplete information of how species might respond to non-analogue situations (Sætersdal *et al.*, 1998). This may lead to the projections of species loss in the southern quarters of the study area being an artifact. This issue has been discussed in some of the bioclimatic envelope modelling papers (eg, Bakkenes *et al.*, 2002; Peterson *et al.*, 2002b). However, only Sætersdal *et al.* (1998) have to our knowledge treated the problem in an explicit manner, by excluding those parts of the study area which were projected to have a future climate with no modern analogue.

It is possible that different types of climatic predictors other than those usually used in bioclimatic modelling might provide better correlations with the species' distributions. Particularly the long-term (eg, 30 years) average data commonly used may not show the effects of certain coincidences, such as a sequence of cool, short summers or growth seasons (Baker *et al.*, 2000). Establishment of, for example, insect populations may depend on very short-term weather events. Moreover, Hill *et al.* (1999) pointed out that mean monthly climate values cannot reflect short-term climatic events and extreme conditions that may have an important influence upon population dynamics of butterflies. A period of particularly wet and cold summer weather may depress local populations to levels where they can be vulnerable to extinction.

A general assumption in bioclimatic modelling is that species' distributions are at equilibrium with current climate. Recent studies have asked how distant from equilibrium are current distributions of species, and further questioned whether possible deviations from equilibrium would produce important biases in species-climate model projections (Svenning and Skov, 2004; Araújo and Pearson, 2005). Using species data from a 50-km grid system in Europe and a pattern-based analysis (Mantel test), Araújo and Pearson (2005) showed that the degree of covariation between four studied species groups and climate varied notably. Covariation was strongest between plant and bird species' composition and climate, whereas the relationships between reptiles, amphibians and climate were weaker. These findings led to the conclusion that the two latter groups would be more likely to have distributions that depart from equilibrium assumptions, possible due to lower dispersal abilities. The authors also concluded that such a departure would affect the reliability in which bioclimatic models capture the full responses of species to climate.

IX Effects of non-climatic factors and scale

In the species-climate modelling literature it has been increasingly highlighted – and

occasionally examined (see Iverson and Prasad, 1998; Pearson *et al.*, 2004; Thuiller *et al.*, 2004a; Virkkala *et al.*, 2005; Luoto *et al.*, 2006b) – that many factors other than climate may have an important role in explaining species' geographical distributions. Such effects need to be taken into account when developing future projections of species' distributions. Iverson and Prasad (1998) showed that in many cases a combination of climate and edaphic variables was necessary to achieve the best CTA models for the studied tree species (see also Coudun *et al.*, 2006). Huntley (1995) proposed that, although an appropriate model relating geographical distribution of plants to environment may include only macroclimatic variables, in the case of birds such a model may need also to include structural attributes and taxonomic composition of vegetation. Crick (2004) emphasized that the current distributions of birds may be due to factors other than climate, for example past persecution (*Milvus milvus* in the UK as an example). In such cases purely species-climate models based on current distributions can yield incomplete indications of the species' climatic needs.

However, most attention has hitherto focused on integrating the possible impacts of land cover into bioclimatic modelling studies. Bakkenes *et al.* (2002) noted that conclusions of the pure species-climate models on coastal regions should be treated carefully because in such regions species' distributions are limited geographically by the sea and not by the climate. In fact, only a few biogeographical studies have explored the importance of climate versus land cover for modelling species' distributions (but see H-Acevedo and Currie, 2003; Stefanescu *et al.*, 2004; Thuiller *et al.*, 2004a; Bomhard *et al.*, 2005). Moreover, it is important to note that the variation of importance of climate and land-cover factors is very likely a scale-dependent phenomenon (cf. Wiens, 1989; Pearson *et al.*, 2004). The relative roles of land cover and scale have been insufficiently examined at different scales (but see Thuiller *et al.*, 2003a). However, the

limited results available so far suggest that, at the coarse European resolution, the predictive power of bioclimatic models are generally not greatly improved by the inclusion of land-cover variables (Thuiller *et al.*, 2004a), whereas at 10 km or higher resolution the integration of land-cover data can improve spatial predictions for certain species (Pearson *et al.*, 2004; Virkkala *et al.*, 2005; Luoto *et al.*, 2006b).

The importance of land cover at varying scales is likely to vary among different groups of organisms and may also be related to the habitat specifity of species. Virkkala *et al.* (2005) showed that the distribution patterns of marshland birds in boreal regions at the scale of 10 × 10 km reflect the interplay between habitat availability and climatic variables; however, the coverage of marshland habitats was clearly the most important predictor for species distributions. Luoto *et al.* (2006a) modelled the distributions of 98 boreal butterfly species at the same resolution using climate and land-cover information. Although certain butterfly species showed clear correlations with some land-cover variables, most of the variation in butterfly distributions appeared to be associated with climate, particularly growing degree-days and mean temperature of the coldest month.

The results of Thuiller *et al.* (2004a), Pearson *et al.* (2004), Virkkala *et al.* (2005) and Luoto *et al.* (2006b) are concordant with the current paradigm that climate governs the species' distributions at broad biogeographical scales (Currie, 1991; Huntley *et al.*, 1995; Parmesan, 1996), whereas land-cover and spatial distribution of suitable habitats determine species' occupancy at finer spatial resolution (Hill *et al.*, 1999; Bailey *et al.*, 2002; Pearson *et al.*, 2004; Luoto *et al.*, 2006b). However, our understanding of how the relative importance of land cover versus climate varies over a range of scales and between different species groups is still incomplete, and more multiscale assessments are needed (cf. Rahbek and Graves, 2001; Rahbek, 2005) if progress in modelling species distributions is to be expected.

X Conclusions

All modelling approaches have their advantages and disadvantages. The choice of the modelling approach has to consider a range of factors including the breadth of ecological knowledge, existing distribution data, spatial and temporal scale as well as goals of the modelling (Pearson and Dawson, 2003). Bioclimatic models allow consideration of how climate change may affect many species simultaneously and provide estimates of potential change in species richness and ecosystems in a given region (eg, Crumpacker *et al.*, 2001; Peterson *et al.*, 2002b; Pearson and Dawson, 2003; Beaumont *et al.*, 2005). These models are useful 'first filters' for identifying locations and species that may be greater risk and provide first approximations as to the impact of climate change on species ranges (Pearson and Dawson, 2003; Thuiller *et al.*, 2005b). Bioclimatic models may also be informative when investigating the likelihood that particular change in climate might affect species' distributions (Araújo *et al.*, 2006). However, due to numerous sources of uncertainty, the models and their results should only be applied with a thorough understanding of the limitations involved (Pearson and Dawson, 2003; Thuiller, 2003; 2004; Araújo *et al.*, 2005a; 2005b).

Sources of uncertainty reviewed here indicate that in applying correlative species-climate models we need to have broad understanding of the wide range of methodological issues that may affect the usefulness of models; only then should we be able to circumvent the pitfalls associated with modelling species responses to climate change. Furthermore, it is clear that more realistic simulations of the impacts of climate change on species range shifts require addressing the complex interactions between the many factors affecting distributions (Pearson and Dawson, 2003). Many recent papers have highlighted the need for research aiming to develop approaches that integrate factors such as land cover, biotic interactions and

dispersal mechanisms into pure species-climate models (Pearson *et al.*, 2002; Guisan and Thuiller, 2005). An increasing number of studies have started to address these challenges (eg, Leathwick and Austin, 2001; Iverson *et al.*, 2004; Pearson *et al.*, 2004; Pearson and Dawson, 2005), but there is still substantial research required. In fact, developing hybrid-models that bring together the best of correlative bioclimatic modelling with the best of mechanistic and theoretical models is one of the most important challenges for modellers (Araújo *et al.*, 2006).

Nevertheless, it is important to acknowledge that natural systems are not closed, hence it is not possible to account for all potential driving forces of species distributions (Araújo *et al.*, 2005a). Thus, errors are an inherent property of bioclimatic models, whether they are correlative, mechanistic or theoretical, and the primary value of models is very likely more heuristic than predictive (Araújo *et al.*, 2005b). By and large, because of the various sources of uncertainty discussed here it may be conceptually inadequate to use the projections of bioclimatic models as face value for making predictions of future events. However, as argued by Whittaker *et al.* (2005), when the limitations of models are understood, we should be in a better position to make the best use of their results. Last but not least, a plea made by Araújo *et al.* (2005b) deserves to be put forward also here: more empirical evidence needs to be gathered to reinforce the confidence of bioclimatic models and their predictions. By providing repeated evidence of their value we should be in a better position to use their outputs with confidence.

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