

BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change

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Abstract

A new computation framework (BIOMOD: BIODiversity MODelling) is presented, which aims to maximize the predictive accuracy of current species distributions and the reliability of future potential distributions using different types of statistical modelling methods. BIOMOD capitalizes on the different techniques used in static modelling to provide spatial predictions. It computes, for each species and in the same package, the four most widely used modelling techniques in species predictions, namely Generalized Linear Models (GLM), Generalized Additive Models (GAM), Classification and Regression Tree analysis (CART) and Artificial Neural Networks (ANN). BIOMOD was applied to 61 species of trees in Europe using climatic quantities as explanatory variables of current distributions. On average, all the different modelling methods yielded very good agreement between observed and predicted distributions. However, the relative performance of different techniques was idiosyncratic across species, suggesting that the most accurate model varies between species. The results of this evaluation also highlight that slight differences between current predictions from different modelling techniques are exacerbated in future projections. Therefore, it is difficult to assess the reliability of alternative projections without validation techniques or expert opinion. It is concluded that rather than using a single modelling technique to predict the distribution of several species, it would be more reliable to use a framework assessing different models for each species and selecting the most accurate one using both evaluation methods and expert knowledge.

Keywords: artificial neural network, BIOMOD, climate change, future climatic envelopes, generalized additive model, generalized linear model, regression tree analysis

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Introduction

Recently documented biotic responses to possible climate and land-use change (Walther *et al.*, 2002; Peterson *et al.*, 2002b; Midgley *et al.*, 2003) raise a crucial question for ecologists and conservationists: Are projected climate and land-use change likely to threaten biodiversity and conservation of species? Several meta-analyses have demonstrated that there is a globally coherent 'fingerprint' of climate change impacts across natural systems and particularly on biodiversity (Parmesan & Yohe, 2003; Root *et al.*, 2003). Static

modelling techniques have been used to assess the impacts of global change on biodiversity distribution, by predicting current species distributions and applying statistical models from current distributions to project future distributions under global change scenarios (for a review, see Pearson & Dawson, 2003). Static modelling relates the current observed distribution of species to a pool of available environmental variables using statistical or rule-based models. Different modelling techniques are commonly applied to project potential future species distributions. Although Generalized Linear Models (GLM) are the most common (Hill *et al.*, 1999; Bakkenes *et al.*, 2002), Generalized Additive Models (GAM) are being used increasingly (Leathwick, 1995; Frescino *et al.*, 2001).

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Alternative rule-based approaches have also emerged as interesting tools to predict current and future potential distributions. These include Classification and Regression Tree analysis (CART) (Rouget *et al.*, 2001; Thuiller *et al.*, 2003b) or Artificial Neural Networks (ANN) (Pearson *et al.*, 2002; Moisen & Frescino, 2002). Modellers have observed that different modelling techniques for the same species may give different results and that different methods tend to vary idiosyncratically across species (Thuiller *et al.*, 2003a). While some comparative studies may guide methodological choices (e.g. Manel *et al.*, 1999; Thuiller *et al.*, 2003a), it may be obscure for non-statisticians or inexperienced users to select a modelling technique to predict species distributions for a specific application.

The purpose of this paper is therefore to present a modelling application, BIOMOD, that allows spatial predictions maximizing the model accuracy and projected future species distributions. Indeed, to predict current species distributions and to project them into the future, it may be necessary to consider more than one modelling technique and use the most accurate one for each species rather than the most accurate across species. In addition, models with similar accuracies for current distributions could have very different behaviour when applying them to future environmental parameter sets. The general framework that is proposed uses different modelling techniques from parametric statistical to non-parametric rule-based (GLM, GAM, CART and ANN) for each species, to predict current species distributions, to evaluate them and then either choose only the most accurate model to make future projections for each species, or keep all the predictions from the different models and project all of them into the future.

Methods

Species data

Sixty-one native tree taxa distributed across Europe were considered for modelling. This covers most of the important timber taxa of Europe, including all the gymnosperm softwoods (Pinales, Taxales and Gnetales) and some hardwoods (Myricales, Juglandales and Fagales) (Humphries *et al.*, 1999). Trees were chosen because: (i) their distribution and ecology is relatively well known compared with other plant taxa; (ii) their richness is correlated (Spearman correlation $\rho = 0.80$, $P < 0.001$) with the overall richness of the Atlas Flora Europaeae (AFE) data set (Araújo & Williams, 2000); and (iii) they are long-lived organisms and their distribution is relatively stable in comparison with

some other groups. The species presence-absence data are a subset of AFE (Jalas & Suominen, 1972–1996), which was digitized by Lahti & Lampinen (1999). Data are located in 4419 UTM (Universal Transverse Mercator) 50×50 -km² grid cells. We used only 2089 grid cells, excluding most of the eastern European countries (except for the Baltic States) because of low recording efforts in these areas (Williams *et al.*, 2000).

Environmental data

The climate data used for analyses are a comprehensive set of bioclimatic variables for Europe from the Climatic Research Unit (<http://www.cru.uea.ac.uk/>) (Mitchell, 2002) (<http://www.pik-potsdam.de/ateam/>): mean annual, winter and summer precipitation, mean annual temperature and minimum temperature of the coldest month, growing degree days ($>5^\circ$) and an index of humidity (mean ratio of annual actual over annual potential evapotranspiration). Means are averaged for the period of 1961–1990. These data sets are supplied on a 10' grid, covering Europe. Then data were aggregated by averaging to 50×50 -km² UTM in order to match the resolution of species data.

To examine future species distributions, I used the climate data obtained in a 10' resolution for 2050 based on the GCM experiments conducted at the UK Hadley Centre for Climate Prediction and Research using the HadCM3 model (Mitchell, 2002) under the SRES scenario A1FI (Nakicenovic & Swart, 2000).

BIOMOD – model calibrations

In order to evaluate the quality of predictions, we divided databases into two subsets: calibration and evaluation. The first, a random sample from 70% of the total database, was used to calibrate (train) the models, whereas the second, comprising the remaining data, was used to evaluate (test) model predictions (Fielding & Bell, 1997). The methods included in the testing framework were GLM, GAM, CART and ANN. GLM are the most commonly used technique in species distribution modelling and have shown good ability to predict current species distributions (Austin & Meyers, 1996; Brito *et al.*, 1999). However, the inability of GLM to deal with complex response curves (Yee & Mitchell, 1991) has stimulated the use of GAM in ecological modelling (Lehmann *et al.*, 2003; Thuiller *et al.*, 2003a). CART are less commonly used than the previous two methods, but are accurate and useful to describe hierarchical interactions between species (Franklin, 1998; Rouget *et al.*, 2001; Thuiller *et al.*, 2003). ANN are being increasingly used (Pearson *et al.*, 2002), but they are still limited by the difficulty in identifying

causal relationships and dominant input variables from the network structure. However, their ability to deal with non-normal statistical distributions and their adequacy to determine environmental envelopes that have non-linear responses to environmental variables offer considerable advantages.

For each species, the following procedures were used:

- (1) **GLM** (McCullagh & Nelder, 1989) with linear, second and third order and polynomial terms (second and third order) with the possibility of interactions only for the linear terms. A stepwise procedure was used to select the most significant variables using the AIC criterion (Akaike, 1974; Anon, 1999).
- (2) **GAM** (Hastie & Tibshirani, 1990) with smooth splines. The degree of smoothness was automatically selected by cross-validation and bounded to 4 for each variable. As for GLM, a stepwise procedure was used to select the most parsimonious model using the AIC criterion (Akaike, 1974; Anon, 1999). GAM being, by definition, additive, interaction terms were not included.
- (3) **CART** (Breiman *et al.*, 1984) using the *rpart* library of Splus (Therneau & Atkinson, 1997). This procedure runs a 10-fold cross-validation to select the best trade-off between the number of leaves of the tree and the explained deviance.
- (4) **ANN** using the library *nnet* of Splus (Venables & Ripley, 2002). This ANN is a feed-forward neural network. ANN was parameterized using seven hidden units in a single hidden layer (selected by cross-validation), with a weight decay equal to 0.03. As each simulation gave slightly different results, the ANN was run 10 times and the mean was used to provide predictions and projections (Ripley, personal communication).

BIOMOD – model evaluations

The accuracy of models was evaluated using two different methods according to their specificity between ‘liberal’ and ‘conservative’ approaches, which have rather different implications in practice (Thuiller *et al.*, in review-b). First, the area under the relative operating characteristic curve (AUC) was computed (for more details, see Thuiller *et al.*, 2003a). This does not require the calculation of a threshold to transform probability values from models to binary presence-absence form (Pearce & Ferrier, 2000; Thuiller *et al.*, in review-b). Second, the κ statistics (Cohen, 1960) was calculated using a threshold optimizing this statistic (Monserud & Leemans, 1992; Thuiller *et al.*, in review-b).

BIOMOD – model predictions and projections

Each model was run for every species, compared and used to derive spatial predictions on the original data (2089 grid cells). Then calibrated models were used to project species distributions using the set of climatic variables for entire Europe at $10' \times 10'$. Potential future distributions were also projected by changing climate as predicted by the HadCM3 GCM under one SRES scenario (A1FI).

To transform probability values from each model, either of the following were used: the threshold maximizing the κ statistics, or the threshold maximizing simultaneously the number of presences and absences correctly predicted (Thuiller *et al.*, in review-b).

Results

Model evaluations

A test of the models was provided by evaluating their accuracy in predicting observed species distributions (Table 1). According to Monserud & Leemans (1992)

Table 1 Mean and standard deviation of AUC and κ statistics for the 61 species for each model, according to the data used

| | AUC | | | | | | | | | κ | | | | | | | | |
|------|------|------|------|------|------|------|------|------|------|----------|------|------|------|------|------|------|------|------|
| | Cal | | | Eval | | | Pred | | | Cal | | | Eval | | | Pred | | |
| | min | me | max | min | me | max | min | me | max | min | me | max | min | me | max | min | me | max |
| GLM | 0.82 | 0.95 | 0.99 | 0.82 | 0.94 | 1.00 | 0.82 | 0.95 | 0.99 | 0.39 | 0.69 | 0.88 | 0.36 | 0.66 | 0.86 | 0.38 | 0.68 | 0.87 |
| GAM | 0.84 | 0.96 | 0.99 | 0.84 | 0.94 | 1.00 | 0.84 | 0.95 | 0.99 | 0.35 | 0.70 | 0.88 | 0.40 | 0.66 | 0.95 | 0.38 | 0.68 | 0.88 |
| CART | 0.83 | 0.94 | 0.99 | 0.54 | 0.87 | 0.96 | 0.82 | 0.92 | 0.98 | 0.45 | 0.72 | 0.88 | 0.27 | 0.59 | 0.84 | 0.45 | 0.68 | 0.86 |
| ANN | 0.87 | 0.97 | 1.00 | 0.82 | 0.95 | 0.99 | 0.85 | 0.96 | 0.99 | 0.54 | 0.79 | 0.94 | 0.34 | 0.68 | 0.84 | 0.50 | 0.75 | 0.89 |

Cal: calibration data; Eval: evaluation data; Pred: original data (calibration + evaluation). min, me and max are, respectively, minimum, mean and maximum values of AUC or κ statistics.

subjective guidelines, κ values above 0.7 can be considered to indicate very good agreement. On average, predicted distributions on both calibration and evaluation data were thus found to exhibit high levels of agreement with observed distributions. Conclusions are similar according to AUC, where subjective guidelines (Swets, 1988) suggest a very good agreement for AUC above 0.9. According to the guidelines presented for the two methods, ANN appeared slightly better than the other methods, while classification trees appeared as the weakest method in terms of discrimi-

Table 2 Percentage of best models across the 61 tree species according to both AUC and κ statistics carried out on evaluation data

| | AUC | κ |
|------|-------|----------|
| GLM | 14.75 | 21.31 |
| GAM | 24.59 | 31.15 |
| CART | 00.00 | 00.00 |
| ANN | 60.66 | 47.54 |

nation ability. Comparing the results for calibration, evaluation and the entire data, the tendency for CART to over-fit during the calibration process resulted in a generally poor agreement for evaluation data (Table 1). ANN also tended to over-fit during the calibration process, but the predictions on evaluation data still showed good agreement. On the other hand, GAM or GLM displayed very small differences in fit between calibration and evaluation data, and thus did not appear to over-fit.

Even if ANN exhibited a higher mean accuracy according to both the ROC curve and κ statistics, there were noticeable differences across species (Table 2). GLM or GAM had a higher accuracy than ANN in several cases, supporting the idea that there is no universal 'best' modelling technique.

Model predictions and projections

Predictions for the 61 modelled species revealed responses that were highly species- and modelling technique-dependent. Generally, the expected trend of

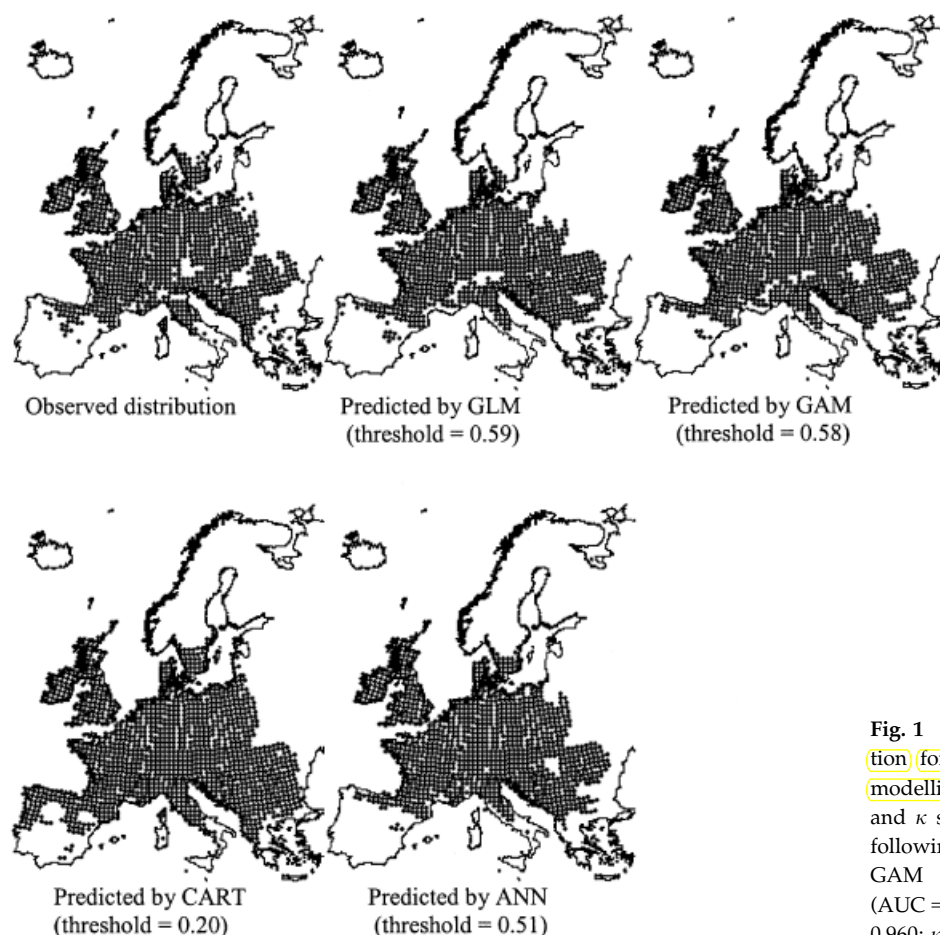


Fig. 1 Observed and predicted distribution for *Quercus petraea* according to the modelling technique used. The ROC curve and κ statistics on evaluation data are the following: GLM (AUC = 0.939; κ = 0.74), GAM (AUC = 0.945; κ = 0.77), CART (AUC = 0.927, κ = 0.76) and ANN (AUC = 0.960; κ = 0.79).

over-fitting by CART was quite obvious, and for a number of species GLM, GAM and ANN differed noticeably. Concerning the projections into the future, the expected trend of northward expansion was apparent for a number of species, but especially for northern native species (e.g. *Betula nana*). However, for many species, changes in potential distribution tended to be multidirectional. To illustrate the study, four species were selected to represent different chorological status in Europe: a Euro-Siberian species (*Quercus petraea*), a continental species (*Castanea sativa*), a Mediterranean species (*Pinus halepensis*) and a Siberian species (*B. nana*).

Predictions of current distribution for *Q. petraea* showed interesting differences according to the modelling technique (Fig. 1). First, even if both AUC and κ yielded similar results across models, they resulted in non-negligible differences in terms of spatial predictions. This indicates that small differences according to the evaluating statistic might translate into significant differences for spatial predictions.

Projections into the future highlighted that small differences for predicting current distributions are exacerbated in the future (Fig. 2). Future distribution projected by CART showed a northward expansion of *Q. petraea* similar to the other three modelling techniques. However, CART predicted a stable distribution in Spain and southern France while the other three methods showed a decrease of suitable conditions in these regions. Even if GLM, GAM and ANN showed similar trends, there were differences in the UK, northern France and Poland. According to the ranking provided by AUC and κ , the future potential distribution of *Q. petraea* projected by ANN should be the most accurate.

Differences between future potential species distributions according to the modelling technique used had a crucial impact to assess the sensitivity of a given species to climate change. For instance, the four models did not result in the same spatial projections in terms of suitable sites lost or gained to the future (Figs 3–5). The impact of climate change for *C. sativa* was different

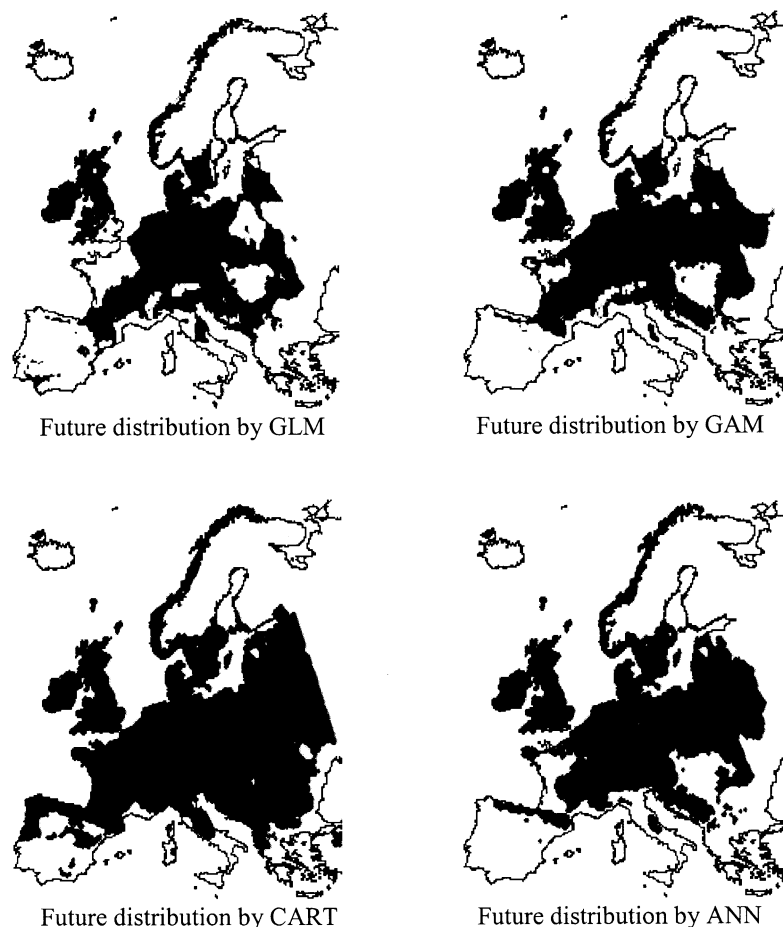


Fig. 2 Projected potential future distribution for *Quercus petraea* according to the modelling techniques. The thresholds used to transform probability values into binary presence-absence form are the same as for Fig. 1.

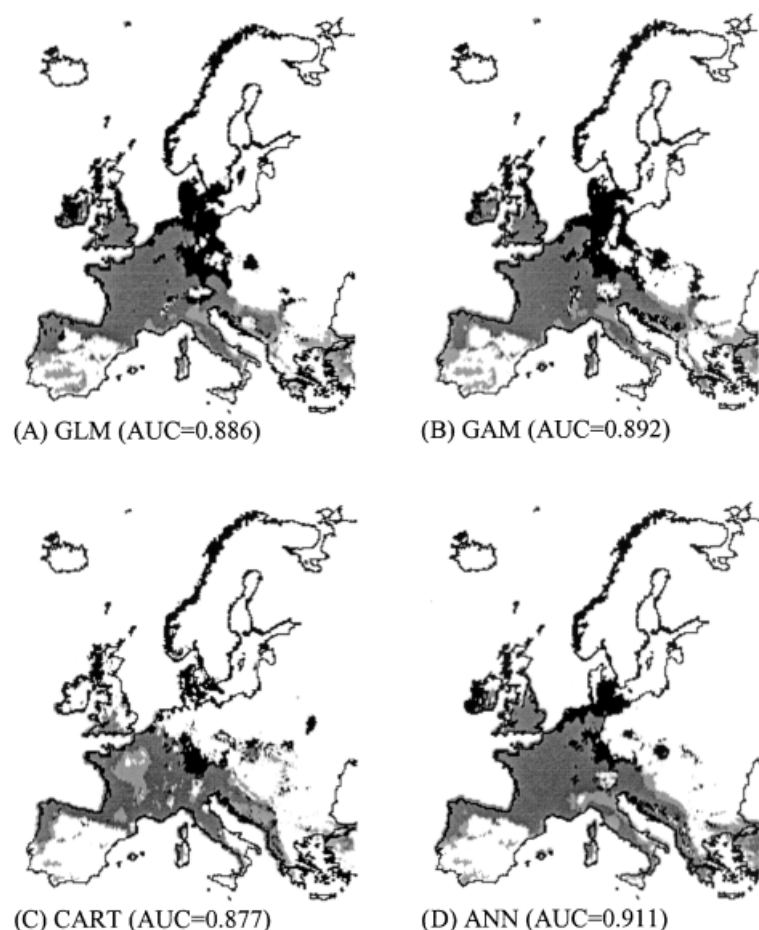


Fig. 3 Comparison of current projected distribution of *Castanea sativa* and its future potential distribution in 2050. Dark grey colour corresponds to stable suitable sites, grey to loss of suitable sites, black to gain of suitable sites and clear grey to stable unsuitable sites.

according to the modelling technique (Fig. 3). CART projected a stable distribution of *C. sativa*, while ANN, GAM and GLM projected a northward expansion and a contraction from southern Europe. For this species, according to the evaluating methods, ANN appeared to be the most accurate model to predict the current distribution and would therefore be the most reliable to generate future projections. Results for *P. halepensis*, a Mediterranean tree, also exhibit substantial discrepancies according to the models used (Fig. 4). For this species, there was a large difference between statistical and rule-based methods. GLM and GAM projected a slight northward expansion with contraction from the extreme southeast and southwest of its current range, while CART and ANN projected only a strong northward expansion without southern contraction. According to the evaluating methods, projection by GAM was the most reliable.

When modelling techniques yield very similar results in terms of accuracy, the results of sensitivity of species

to climate change show similar patterns. This was the case, for example, for *B. nana*, a Euro-Siberian species that was projected to lose a considerable amount of suitable habitat in the southern part of its distribution almost identically by all modelling techniques (Fig. 5).

Discussion

Results presented in this study suggest that the reliability of future potential species distributions depends strongly on the modelling technique used. A small difference between two modelling techniques in terms of AUC or κ can result in a large difference in projections of future potential habitat. It is worth noting that only a subsample of possible forms for GLM, GAM, CTA and ANN was used. The way in which the different modelling techniques in BIOMOD were parameterized is explained and detailed here and in other papers (Thuiller *et al.*, 2003a,b). However, there are different methods to parameterize these models; for

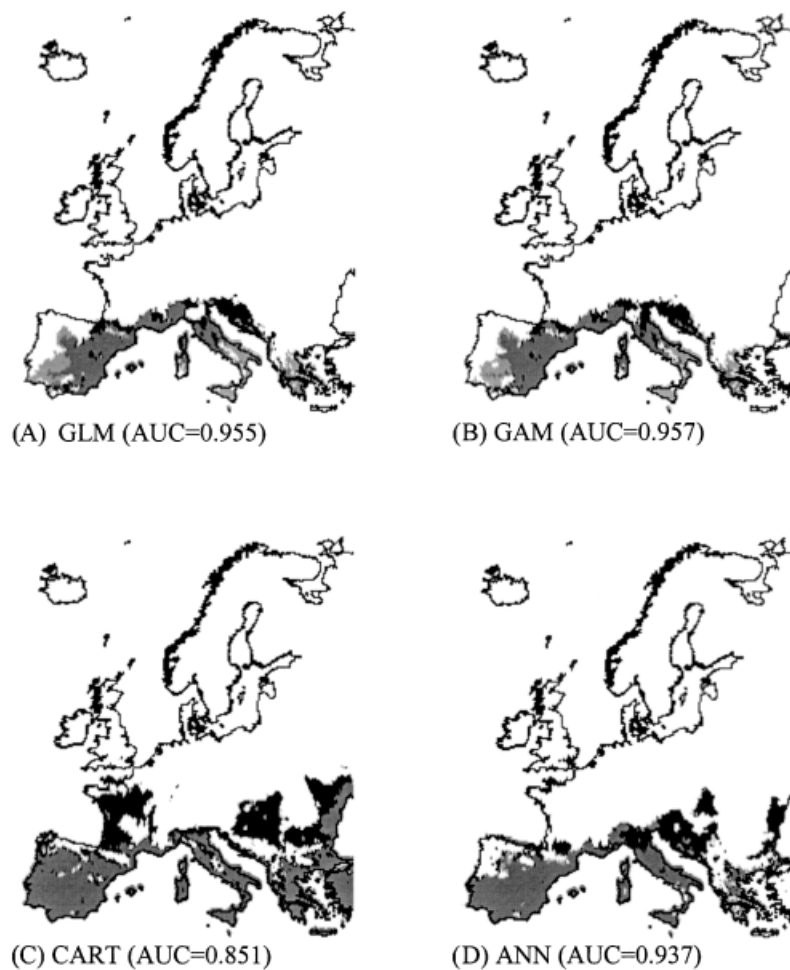


Fig. 4 Comparison of current projected distribution of *Pinus halepensis* and its future potential distribution in 2050. Dark grey colour corresponds to stable suitable sites, grey to loss of suitable sites, black to gain of suitable sites and clear grey to stable unsuitable sites.

instance, using lowess smoother for GAM instead of spline, using only linear terms in GLM, or using a higher number of hidden network units in ANN. A sensitivity analysis would be worthy to assess the importance of such parameters, but this was clearly beyond the scope of this paper. Moreover, if differences also exist according to the methods to fit a single model, it enhances the use of a framework such as BIOMOD that tests different models and chooses the most accurate one. BIOMOD could be used to test the same modelling technique, but with different forms and parameterizations. Readers interested in more detailed discussions and model comparisons could refer to Brotons *et al.* (in review), Franklin (1998), Guisan *et al.* (1999), Vayssières *et al.* (2000) and Thuiller *et al.* (2003a). All these papers compared several methods and aimed to identify the most accurate overall. Even when using three sets of data at different locations, scales and resolutions, there was no evidence that any particular

technique was consistently better than any other (Thuiller *et al.*, 2003a). Here, an alternative approach that uses different modelling techniques within a single framework has been proposed, where running all of them provides accurate current predictions and reliable future projections. Other modelling techniques could be added to this framework. For instance, genetic algorithms as used by Peterson and co-workers (Stockwell & Peters, 1999; Peterson *et al.*, 2001, 2002a) could be integrated into this framework to cover an even larger spectrum of modelling techniques.

If the aim of a study is to perform only predictions on current data, BIOMOD is useful because it selects the most accurate modelling technique for each species. In this sense, predictions are optimized as compared with other approaches using only one *a priori* modelling technique. Of course, for some species and locations, the different modelling techniques could give exactly the same results, and thus extra calculation time to run

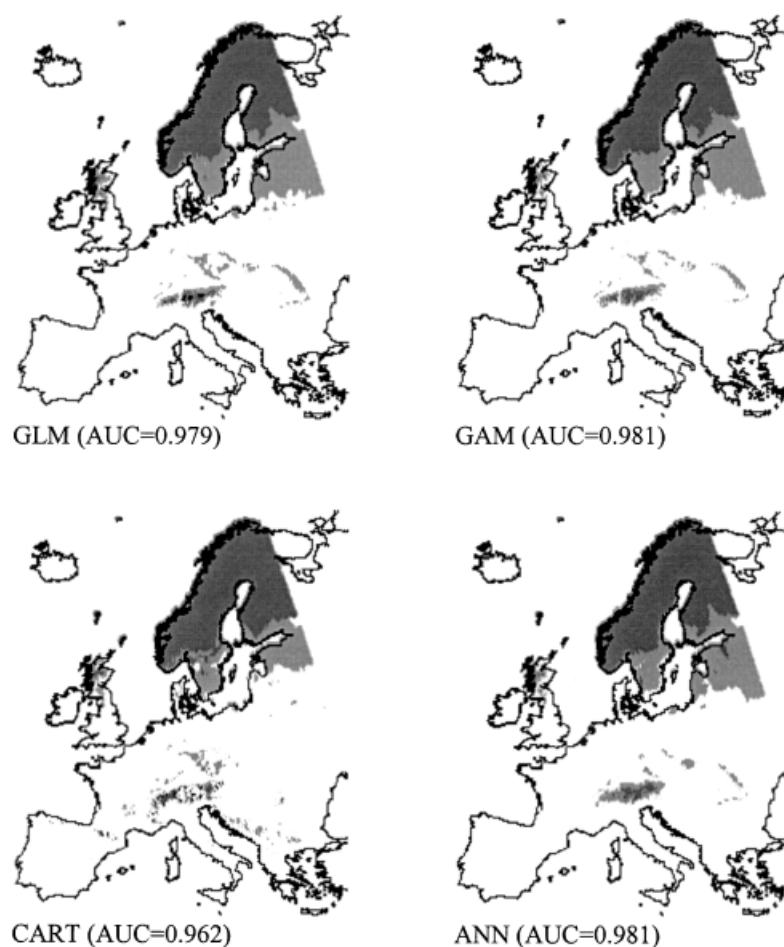


Fig. 5 Comparison of current projected distribution of *Betula nana* and its future potential distribution in 2050. Dark grey colour corresponds to stable suitable sites, grey to loss of suitable sites, black to gain of suitable sites and clear grey to stable unsuitable sites.

different models would be unnecessary (for instance, GLM, GAM and ANN for *B. nana*).

Another advantage of BIOMOD is with respect to projections of species distributions under climate change scenarios. Indeed, it is impossible to gate whether projected future potential distributions are accurate or not, or if one method is better than another, even if expert knowledge could help to assess the reliability of projections. Two alternatives are then possible:

- Either, decide to trust the evaluation process, select for each species the most powerful modelling technique to predict current distributions and project future potential distributions.
- Or, carry out predictions and derive projections of future potential distributions using all the modelling techniques employed (i.e. Figs 2–5) and draw conclusions by comparisons across outputs. These conclusions and validations could be based on expert

knowledge or published studies. A complementary way is to analyse projected future response curves to environmental gradients to identify unrealistic patterns generated by particular modelling techniques (Thuiller *et al.*, in review-a).

Alternatively, the best approach to assess a model's accuracy in the future would be to evaluate models retrospectively to produce projections of the present-day distribution for data gathered in the past. Unfortunately, accurate past data of species and climate are not readily available for Europe at this point.

Projections of potential future distributions also need to be interpreted with caution. If any model is used to project outside the range over which it has been fitted, projections could be less reliable (Thuiller *et al.*, in review-a). Even if models presented in this study are quite accurate and commonly used to assess the impact of global change (Sykes, 2001; Bakkenes *et al.*, 2002; Pearson *et al.*, 2002), particular care should be taken for

species at the edge of their distributions in the study area and for which models can therefore not capture the entire suitable environmental range.

I conclude by proposing to use a large spectrum of methodological approaches (parametric, non-parametric, rule-based or machine learning) to have a wide array of possible future species distributions and assess their reliability using (i) the evaluation methods and (ii) expert knowledge and ecological validation. BIOMOD could also be used to assess the uncertainty of projections of future species distributions. At least three sources of uncertainties are inherent to the modelling process presented in this paper and other published studies (Bakkenes *et al.*, 2002; Berry *et al.*, 2002; Midgley *et al.*, 2002; Peterson *et al.*, 2002b): the uncertainty based on the climate change scenarios, the uncertainty based on the modelling techniques and the uncertainty based on the selection of the threshold to transform probability values into presence-absence form. The framework presented in this paper could measure the prevalence of these three sources of uncertainties and in this sense evaluate the reliability of projections of future species distributions.

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