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Original article

Predicting range shifts of northern bird species: Influence of modelling technique and topography

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ABSTRACT

Using eight modelling techniques, bird atlas data of Finland and northern Norway, and data on 'current' climate (1971–1990) and projected future climate (2051–80; climate scenarios HadCM3 A2 and B1), we forecasted current and future distributions of 28 land bird species in northern Europe. Specifically, we investigated (i) the impact of inclusion of topographical information on the pure bioclimatic envelope models ('climate -only' models), (ii) the accuracy and spatial differences of the predictions from the different models, and (iii) the co-occurrence of hotspots in species numbers and proportion of protected areas, both currently and in the future. Modelling accuracy was measured as the cross-validation area under the curve (AUC) of the receiver operating characteristic plot. Generalized additive models (GAM) and generalized boosting method (GBM) gave parallel projections with high predictive accuracy for the species distributions and their hotspots, but random forests (RF) and artificial neural networks (ANN) also showed good model performance. Inclusion of topographical variables showed an overall tendency to increase the accuracy of the climate-only models, and this increase was statistically significant in GAM, GLM (generalized linear models) and RF. According to both climate-only and climate-topography models, coincidence of grid cells harboring species hotspots and larger protected areas appears to decline by 2051-80. This calls for further evaluation of the adequacy of the reserve network in northern latitudes, where species are probably particularly susceptible to the effects of climate changes.

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1. Introduction

Global climate change is increasingly affecting species populations and communities (Parmesan, 2006), and future changes in climate are projected to cause considerable changes in the distribution of species representing several different taxa (Beaumont and Hughes, 2002; Thomas et al., 2004; Thuiller et al., 2005a). In Europe, bird species distributions have been forecasted to change considerably in the 21st century due to climate change (Huntley et al., 2007).

Bioclimatic envelope models are increasingly employed to assess the potential impacts of climate change on species distributions (Pearson and Dawson, 2003; Guisan and Thuiller, 2005; Heikkinen et al., 2006). These models are a special case of niche-based or species distribution models using climatic predictors only (Guisan and Thuiller, 2005), based on the finding that on broad spatial scales climatic variables appear to be good predictors of species distributions (Pearson and Dawson, 2003; Pearson et al., 2004; Thuiller et al., 2004; Huntley et al., 2007). Modelling algorithms are employed to define the relationships between present-day distributions of species and current climatic variables (i.e. models). Once established, the models are then used to simulate the potential future distributions of species and investigate possible decreases of suitable climate space for species under different climate change scenarios (Thuiller et al., 2005a; Heikkinen et al., 2006, and references therein; Luoto and Heikkinen, 2008; Virkkala et al., 2008).

However, although bioclimatic envelope models can provide useful first approximations of the direction and magnitude of the range shifts of species, they have a number of limitations (Pearson and Dawson, 2003; Heikkinen et al., 2006; Lawler et al., 2006; Luoto et al., 2007). In this study we address two of the potential limitations. First, an increasing body of evidence suggests that the projections of species distributions derived from bioclimatic envelope models may vary considerably depending on the modelling technique applied (Segurado and Araújo, 2004; Elith et al., 2006; Lawler et al., 2006; Pearson et al., 2006).





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Many comparative modelling studies have come to the conclusion that no single modelling method will always provide the most accurate predictions for all species (Thuiller, 2004). Consequently, it is now commonly considered that evaluating the potential impacts of climate change on species ranges should be based on outputs from more than one modelling technique (Thuiller, 2004; Araújo and New, 2007; Marmion et al., 2009a). The appearance of similar trends among projections from multiple modelling techniques, in other words agreement among the model outputs, may help in identifying the most plausible direction and magnitude of the potential future range changes of species (Araújo et al., 2005a; Araújo and New, 2007; Marmion et al., 2009a; but see Algar et al., 2009).

Second, in contrast to the impacts of modelling techniques, the consequences of disregarding topography (in essence, topographical heterogeneity) for the outcomes of bioclimatic envelope models have been investigated only rarely [but see (Peterson, 2003; Luoto and Heikkinen, 2008; Trivedi et al., 2008; Ashcroft et al., 2009)]. Luoto and Heikkinen (2008) observed that the inclusion of elevation range increased the predictive accuracy of climate-only models for 86 European butterfly species out of 100. The differences in projected future distributions were most notable in mountainous areas, where the climate-topography models projected only about half of the species losses compared to the climate-only models. Thus, disregarding topographical heterogeneity may cause a significant source of error in broad-scale bioclimatic modelling, but more research is clearly required to assess the potential magnitude of this factor in different regions and at different spatial resolutions (Randin et al., 2009).

In this work we extend the study of Virkkala et al. (2008) in three important ways. First, we fit eight different modelling approaches to the bird species and climate data in order to evaluate whether the projections from different methods are concordant, and what is the accuracy of the species-climate models for the studied 28 bird species provided by different techniques. Second, following Luoto and Heikkinen (2008) we include topographical heterogeneity into the modelling in order to investigate whether this inclusion improves the model performance and alters interpretation of the results. Third, we also evaluate the outcomes of different models from a conservation biological aspect. Investigation of the effectiveness of the reserve network in northern Europe in capturing the projected hotspots of bird species, both now and in the future, will be an important research topic. The predicted increase in temperature will probably be particularly dramatic in the northern latitudes (IPCC, 2001). For example, based on the A2 scenario the temperature increase in the Arctic is expected to be 7 °C by 2100 on average, with wide regional variation (ACIA, 2005). Therefore, species particularly susceptible to the effects of climate warming are those with distributions concentrated in the northern boreal or arctic zones (Virkkala et al., 2008). Moreover, the northern birds will apparently be in double jeopardy because their projected future range will contract dramatically, as the Arctic Ocean will effectively limit their range expansion northwards.

2. Material and methods

2.1. Study area

The study area consisted of two spatially hierarchically delimited areas. First, we used the bird data from Finland and Finnmark (the northernmost county of Norway) for establishing the bioclimatic envelope models for each of the bird species included in the study (Fig. 1). This 'core' part of the study area ranged from the Baltic Sea to the Arctic Ocean, between 59° 50′ N and 71° 5′ N and between 20° 35′ and 31° 35′ E. Second, we applied the bioclimatic models constructed for the studied species (based on the data from the core study area) to generate predictions of bird species distributions over a wider area covering parts of adjacent regions in Sweden, Norway and Russia (Fig. 1B).

The main part of the study region has a boreal climate, with a decrease in rainfall and temperature from the southwestern Finnish hemiboreal zone (mean annual temperature ca. 5 °C and mean annual precipitation 600–700 mm) to the continental subarctic and arctic Finnmark (-2 °C and 400 mm). In the coastal zone of Finnmark winters are much milder, with an annual mean temperature of over 3 °C and also with higher annual precipitation, even above 700 mm.

Biogeographically Finland stretches through the boreal coniferous vegetation zone, which is dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Ahti et al., 1968). The northern boundary of spruce forest is in northern Lapland (the northernmost county of Finland) and that of pine forest in southern Finnmark. Mountain birch (*Betula pubescens czerepanovii*) forms the northernmost forests and constitutes the tree line in the mountains of northern Finland and Finnmark. The landscape in Finland is largely dominated by forests and mires. In northernmost Finland and in Finnmark there are mainly gently sloping mountains with treeless heath vegetation.

2.2. Bird data

We included 28 land bird species in our analyses: 11 species breeding and/or foraging primarily in forests, 11 in mires, and 6 in mountain heaths (Appendix A). 19 of the species were migratory and 9 resident or irruptive. All the studied species had their southern range boundary in Finland (Hagemeijer and Blair, 1997; Väisänen et al., 1998).

We used the pooled information of two bird atlas surveys carried out in Finland in 1974–79 and 1986–89 (Väisänen et al., 1998). The bird atlas for the northernmost county of Norway, Finnmark (field work 1977–86) (Frantzen et al., 1991) was also included in the data. Both the Finnish and Finnmark atlases used 10×10 km grids, in which observations of species were recorded.

For Finland, a given bird species was considered as breeding if it fell into one of the categories 'breeding possible', 'breeding probable', or 'confirmed breeding' (Väisänen, 1989). Only those 10-km grid cells in which the survey activity of atlas surveys was graded as 'fair survey', 'satisfactory survey of the square', 'well surveyed' or 'thoroughly surveyed square' (Väisänen et al., 1998) were included in the model calibration data set. In Finnmark no such classification of survey activity was available. However, to avoid squares with only occasional observations we took into account all squares in which any of the studied species were observed with probable or confirmed breeding of any other species.

Because climate data in northern Europe was available only for $10' \times 10'$ grid cells, the original bird records collated using the 10×10 km grid system were transformed into the $10' \times 10'$ grid system. A cell in the $10' \times 10'$ grid was interpreted as being occupied by a species when the original occupied 10 km grid cells covered at least 40% of the 10' cell. When the data from Finland and Finnmark were combined, the same $10' \times 10'$ grids were applied.

Coastal grid cells with small land area were excluded because of lack of climate data. The original data used as a basis for developing bioclimatic envelope models included 2655 cells of 10' (Fig. 1B). The data from Finnmark are not as extensive as those from Finland (Fig. 1B). However, we consider that the Finnmark data are representative enough for our predictive modelling, as well as useful as it complements the knowledge of the distribution of the study



Fig. 1. A. Location of the study area in northern Europe. B. $10' \times 10'$ grid cells with atlas data used in Finland and Finnmark (n = 2655; i.e. the core study area used in model building, shown with darker grey) and the larger region (lighter grey) to which the bioclimatic models were applied and including parts of Sweden, Norway and Russia in addition to the core area (no. of grid cells = 3901).

species in the northernmost parts of the study area. The distribution patterns of species are spatially predicted based on climate and topographic data, and therefore total coverage of studied squares is not inevitable. The most common species in the data was the brambling (*Fringilla montifringilla*), with a prevalence of 92.1%, and the rarest was the horned lark (*Eremophila alpestris*, prevalence 1.2%, see Appendix A).

2.3. Climate data

The climatic data included mean values for the period 1971–1990 and projected mean values for 2051–2080 for all climatic variables. The projected climate scenario data were taken from the general circulation model HadCM3 General Circulation Model with a 10' resolution and included two emission scenarios: B1 and A2 (Mitchell et al., 2004), as compiled in the EC FP6 Integrated Project ALARM (Settele et al., 2005). The two emission scenarios were used to estimate low and high expected change in climatic conditions. In the B1 scenario the projected average change in mean temperature by 2100 is 2.0 °C and in the A2 scenario 3.8 °C (IPCC, 2001). According to B1 the atmospheric concentration of CO₂ is expected to increase from the present 380 parts per million (ppm) to 530 ppm and in A2 to 860 ppm by 2100.

We focused on four climate variables which are known to affect breeding and overwintering of bird species in northern regions: mean temperature in April–June, precipitation in April–June, mean temperature of the coldest month and precipitation in December–February (Forsman and Mönkkönen, 2003; Virkkala et al., 2008). The significance of each of these variables in explaining the distribution of the studied bird species in 1971–90 was studied and the significant explanatory variables were used in delimiting a bioclimatic envelope for each species (see Virkkala et al., 2008).

In April–June temperature there is a clear gradient from south to north, while the precipitation gradient is mainly west-east (Fig. 2, A–D). Comparison of the observed climate data and the projected values for 2051–2080 shows that both spring

temperature and spring precipitation are predicted to increase in the future.

2.4. Topographical data

As topographical variables, elevation range in each cell was included in the analyses and mean altitude above sea level was used in interpreting the modelling results (Fig. 2E and F). Protected area data were extracted from the World Conservation Monitoring Centre (WCMC) database (2006). Following Araújo (2004), a 10' grid cell was regarded as protected if at least half of its land area was included in the protected area.

2.5. Statistical analyses

We predicted the distribution of the 28 northern land bird species using the BIOMOD framework developed for the R environment (Thuiller, 2003). BIOMOD includes eight different modelling techniques:

- (1) Generalized linear models (GLM) are mathematical extensions of linear models (McCullagh and Nelder, 1989) which can handle nonlinear relationships and different types of statistical distributions characterizing spatial data, and are technically closely related to traditional practices used in linear modelling and analysis of variance (ANOVA). For each of the 28 bird species, linear, 2nd and 3rd order polynomial terms were computed to provide the probability of occurrence in each grid square, as a response to the four climatic variables and the elevation range. An automatic forward stepwise procedure is used by BIOMOD to compute the best model by minimizing the Akaike information criterion (AIC) value (Thuiller, 2003).
- (2) Generalized additive models (GAM) (Hastie and Tibshirani, 1990) are nonparametric extensions of GLM, and are often used in biogeographical studies (Guisan et al., 2002; Thuiller et al., 2006). GAM provide a flexible data-driven class of



Fig. 2. Mean spring (April–June) temperature (°C) and precipitation in 1971–90 (A, C, respectively) and predicted mean spring temperature and precipitation in 2051–80 (B, D, respectively) based on the A2 climate scenario. E = mean altitude (m) and F = elevation range (m) in each 10′ grid cell.

models based on a cubic-spline smoother with four degrees of freedom that permit both linear and complex additive response shapes, as well as combination of the two within the same model. The smooth functions are computed independently for each explanatory variable and added to construct the final model. The step forward variable selection of GAM in BIOMOD is based on AIC (Thuiller, 2003).

- (3) Classification tree analysis (CTA) is an alternative to regression techniques. It is based on classification trees (Breiman et al., 1984) and uses recursive partitioning to split the data into progressively smaller, homogenous, subsets until a termination is reached (Venables and Ripley, 2002). The optimal length of the tree is selected by a 10 cross-validations procedure. The advantage of CTA is that it allows capturing of non-additive behavior and complex interactions.
- (4) Artificial neural networks (ANN) are an advanced and powerful machine learning method, capable of handling nonlinear relationships (Lek and Guegan, 1999). We used a singlelayer perceptron without skip-layer connections. Therefore, the related feed forward neural network contains three different layers: the input layer (in which the environmental variables are input), the hidden (intermediate) layer and the output layer. Each layer is composed of independent neurons, each of which treats separately the outputs of all neurons from the previous layer as inputs of multivariate linear functions. The process is continued until processing of the output layer. To avoid overfitting in neural networks, a fourfold cross-validation method was implemented to stop training of networks. This four-fold cross-validation process is also used to set the optimal amount of neurons in the hidden layer (i.e. equals either to 75% or to 100% of the amount of explanatory variables) and to optimize the weight decay (0.01, 0.05 or 0.1).
- (5) Multivariate adaptive regression splines (MARS) combines classical linear regression, mathematical construction of splines and binary recursive partitioning to produce a local model in which relationships between response and predictors are either linear or nonlinear (Friedman, 1991; Leathwick et al., 2006; Elith and Leathwick, 2007). A pre-processing algorithm transforms the environmental variables into a new set of variables. Then, MARS performs successive approximation of the system using different intervals of the transformed variables ranges, by a series of linear regressions.
- (6) Mixture discriminant analysis (MDA) (Hastie and Tibshirani, 1996) is an extension of linear discriminant analysis (LDA) (Venables and Ripley, 2002). MDA assumes that the distribution of the class of each environmental variable follows a Gaussian distribution. MDA enhances the LDA, allowing the classifier to handle different prototype classes such as a mixture of Gaussians. The environmental parameters form primal classes, which are divided into sub-classes. The classification results from these subclasses, a mixture density, describe the distribution density of the primal classes of environmental variables. The number of sub-classes was deduced from the variation of the calibration (training) data. An independent observation was then classified into the class, maximizing its probability to belong to this particular class (Ju et al., 2003; Bashir and Carter, 2005). Here, the scaling process of MDA is optimized by using a regression method based on MARS (Thuiller et al., 2009).
- (7) Random forest (RF) (Breiman, 2001; Cutler et al., 2007) is a machine learning method. Random forest generates hundreds of random trees. A selective algorithm limits the number of implemented parameters in each tree. A training set for each tree is chosen as many times as there are observations,

among the whole set of observations. After the trees have been built, data are entered into them and each grid square is classified by all the trees. At the end of the run, the classification given by each tree is considered as a "vote", and the classification of a grid square corresponds to the majority vote among all trees (Breiman, 2001; Prasad et al., 2006).

(8) Generalized boosting method (GBM) is highly efficient in fitting the data, is non-parametric and combines the strengths of different modern statistical techniques (Ridgeway, 1999). Here, GBM was implemented into R (R Development Core Team, 2004) using the library GBM (Generalized Boosted Regression Modelling). GBM is based on the Gradient Boosting Machine developed by Friedman (2001). Boosting is a numerical optimization technique for minimizing a loss function (such as deviance) by adding at each step a new tree that best reduces the loss function (Ridgeway, 1999; Elith et al., 2008). Environmental variables are input into a first regression tree, which maximally reduces the loss function. For each following step, the focus is on the residuals. For example, at the second step a tree is fitted to the residuals of the first tree. The model is then updated to contain two trees, and the residuals from these two trees are calculated. The sequence is repeated as long as necessary (Elith et al., 2008). The maximum number of trees was set to 3000, and a 10 cross-validations procedure was performed.

We examined the predictive power of the derived models based on an evaluation data set, spatially mixed (random split 30%) with the calibration data set (70%) and assessed the predictive power of the models with the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding and Bell, 1997). An approximate guide for classifying the accuracy of models using AUC is (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.

Using the outputs from the different models, the original data of species presence were extrapolated to a larger region, including areas in northern Sweden, northern Norway and north-western Russia connected to the core study area for the periods 1971–90 and 2051–2080 (Fig. 1B). This area of projected presence of species covered a uniform area of 3901 grid cells. The models provided probability values of occurrence in a cell for each species. When converting the probability values into presence-absence records of species in a cell, a threshold based on the original prevalence of species in the calibration data set was used (Liu et al., 2005). Thus, if in the calibration data set, the original prevalence of a species had been e.g. 30%, then the cut-off value of the probability of presence in the predicted data sets would be 0.30.

We compared the simulated species distributions in 1971–1990 to those in 2051–2080, and calculated the climatically suitable area for each species in both periods based on predicted presenceabsence, as derived from the eight models. The sums of climatically suitable areas (i.e. areas where species were predicted to be present) were compared (subtracted) between the latter period and that of 1971–1990, so that higher negative values in percentage change indicated higher loss of climatically suitable area (or positive values gain of suitable area).

Finally, we identified spatial hotspots for the studied 28 bird species in our study area, both for current and future time periods. Hotspots were delimited as the set of 10' grid cells that contained the highest 5% of species numbers in a given period (Prendergast et al., 1993). The proportions of the protected area of 10' grid cells in the 5% hotspots were compared between the time periods in the different models. These 5% hotspots in protected areas are regarded here as an example of the application of these modelling techniques.

Table 2

3. Results

The predictive accuracies (AUC values from the split-sample evaluation) of the eight models based on climate variables and both climatic and topographical variables for the studied 28 bird species are presented in full in Appendices B and C, and summarized in Table 1. For all the modelling techniques the number of species with poor performance in AUC varied between 0 and 4 in the analyses. Species with the lowest mean AUC values included species such as hawk owl Surnia ulula (mean AUC in the eight climate-only models 0.71, and in climate-topography models 0.72), Arctic warbler Phylloscopus borealis (mean AUCs 0.72 and 0.73), two-barred crossbill Loxia leucoptera (mean AUCs 0.72 and 0.72), and great grey owl Strix nebulosa (mean AUCs 0.73 and 0.74) (see Appendices B and C). The highest species numbers with excellent AUC performance (9) were in GAM and GLM in climate-topography models (Table 1). On average, analyses including climate-topography variables had higher predictive performance than those with climateonly variables for all models except ANN and MARS. This general trend is obvious in the comparison of the 224 pairs of climate-only and climate-topography models developed for the studied 28 species, where climate-topography models showed higher AUC values than climate-only models in 120 cases and the number of opposite cases was 75 (Table 2). However, as regards individual models, statistically significantly higher AUC values occurred only in GAM, GLM and RF (Table 2).

There was considerable variation between the outputs from the different models. The results of ANN, CTA, GAM, GBM and GLM were mainly concordant and predicted 66-93% (mean = 80.5%) net loss in area in climate-only models and 65–90% (mean = 75.6%; difference: z = 2.023, p = 0.043, Wilcoxon signed rank test) net loss in climate-topography models in scenario A2, and 56-87% (mean = 73.8%) and 57-85% (mean = 69.8%); difference: z = 1.753, p = 0.080, Wilcoxon signed rank test) net losses in scenario B1, respectively (Table 3). By contrast, MARS showed an increase in the numbers of cells occupied in both climate-only and climatetopography variables in both scenarios. RF showed an increase in occupied cells in climate-topography variables and a slight decrease (4–5%) in climate-only variables in both scenarios. The results of CTA suggested the highest number of species 'extinctions' (i.e. total loss of climatically suitable area), 4–8 species depending on the variable group or scenario. The significance of including topography variables varied between species and modelling techniques: for example, the rustic bunting Emberiza rustica showed almost equal results in climate-only and climate-topography variables in GBM, whereas in the brambling the results varied between climate-only and climate-topography variables in GAM (Fig. 3).

Table 1

Distribution of the 28 northern bird species in different accuracy classes of area under the curve (AUC, based on cross-validation) with respect to eight modelling techniques (mean) with climate-only variables and climatic and topographical variables.

Model	Climate-only		Climate-top	Climate-topography				
	Excellent	Fair Poor		Excellent	Fair	Poor		
ANN	7	21	0	8	19	1		
CTA	3	23	2	5	19	4		
GAM	6	22	0	9	19	0		
GBM	3	25	0	4	24	0		
GLM	4	24	0	9	19	0		
MARS	5	23	0	5	21	2		
MDA	4	22	2	5	22	1		
RF	5	23	0	8	20	0		

Rating of the model accuracy classes (Swets, 1988): excellent = AUC >0.9, fair = 0.7 < AUC < 0.9 and poor = AUC < 0.7.

Significance of comparisons in the accuracy of different models based on climateonly variables (AUC_{cli}) and climatic and topographical variables (AUC_{clitopo}).

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Model	AUC _{cli}	AUC _{clitopo}	z	р	Ranks
ANN	0.845	0.841	1.214	0.225	9/18/1
CTA	0.820	0.821	0.719	0.472	9/9/10
GAM	0.836	0.846	2.573	0.010	19/5/4
GBM	0.836	0.840	1.416	0.157	16/8/4
GLM	0.831	0.841	3.231	0.001	19/6/3
MARS	0.829	0.824	0.711	0.477	16/10/2
MDA	0.809	0.813	0.495	0.620	12/14/2
RF	0.846	0.855	3.163	0.002	20/5/3

Ranks: positive/negative/tied, positive or negative refer to climate-topography variables (Wilcoxon signed rank test).

Fig. 4 shows the spatial shift of 5% hotspots of cells in terms of species numbers between 1971–90 and 2051–2080 based on the A2 scenario in climate-only and climate-topography variables. The general pattern of shift in hotspots of these northern species is westwards and upwards along the elevation gradient. However, MARS deviate clearly from the general patterns, as do partly also MDA. The hotspots defined by MARS move considerably to the south in both the analyses, as do hotspots defined by MDA in the models based on climate-topography variables. Between the other models (ANN, CTA, GAM, GBM, GLM, RF), variation in the change of length and direction of the 5% hotspots is much smaller in the analyses (Fig. 4).

The proportion of the predicted distribution of hotspots coinciding with grid cells with larger protected areas varied between 24 and 57%, with a mean of 50% based on climate-only variables and 41% based on climate-topography variables overall the models (Table 4). The predicted proportion situated in protected areas declines, being on average 39% in climate-only and in climatetopography models both in the A2 and B1 scenarios.

4. Discussion

4.1. Modelling techniques, species characteristics and scale

A general outcome of model comparisons has been that the most novel modelling techniques, such as RF and GBM, outperform the most established techniques (Elith et al., 2006; Lawler et al., 2006; Cutler et al., 2007). In our analyses RF also achieved the highest (split-sample evaluation) AUC-values of the modelling techniques both in climate-only and climate-topography variables, and GBM was included among the three most accurate techniques. RF was specifically advocated for bioclimatic envelope modelling by Lawler et al. (2006) as a modelling method that may provide robust predictions of range shifts of species in the face of climate change. In addition, a recent study by Marmion et al. (2009a) showed that for many species RF may provide equally high predictive accuracy as certain consensus methods, probably because RF inherently incorporates the concept of ensemble forecasting (Araújo and New, 2007). In a comprehensive model comparison study, Elith et al. (2006) concluded that the good performance of GBM is due to its ability to combine the strengths of regression trees, namely omission of irrelevant variables and ability to model interactions, with those of boosting, i.e. the building of an ensemble of models that generally approximate the response surfaces more accurately than single models. Artificial neural networks also showed a good model performance in our study, which is in agreement with the results of Araújo et al. (2005b) and Sharma and Jackson (2008).

However, the most problematic part in bioclimatic modelling is applying the models to predict potential future distributions,

274

Table 3

RF

25.6

Model Climate-only Climate-topography Prevalence % Change % Gain % Loss % No. sp extinct Prevalence % Change % Gain % Loss % No. sp. extinct A2 ANN 79.0 14.9 -66.3 [-99.1; +143.1] 10.9 14.5 -70.5[-99.3; +58.1]8.6 0 77.1 0 CTA 5.0 -91.4 [-100.0: -52.9] 1.3 92.7 7 7.7 -84.3 [-100.0: 0.0] 1.5 85.8 8 7.3 87.2 3 8.1 -73.3[-100.0: +230.2]GAM -82.0[-100.0; +2.6]5.2 14.0 87.4 3 3 GBM 3.9 -92.7 [-100.0: -51.9] 1.9 4.2 -89.5 [-100.0: -10.0] 91.1 4 94.6 1.7 GLM 12.4 -65.9[-100.0; +100.3]18.3 84.2 3 12.0 -64.8 [-100.0; +102.6] 20.5 85.3 3 MARS 32.4 +9.2 [-98.4; +453.2] 68 1 58.8 0 434 +30.3[-99.7; +500.0]786 483 0 MDA 258 -21.0[-91.4; +151.4]43.0 640 0 176 -467[-893 + 237]118 58 5 0 RF 23.8 -4.7 [-97.3; +299.1] 62.7 67.4 0 26.6 +14.9[-86.7; +397.1]71.5 56.6 0 B1 ANN 0 -57.6 [-98.6: +128.5] -68.1 [-98.3: +11.7] 6.3 18.7 10.5 68.1 0 15.3 74.3 CTA 7.7 -86.1[-100.0; -30.3]1.8 88.0 4 10.3 -79.3 [-100.0; 0.0] 2.2 81.5 5 2 GAM 112 -71.8 [-100.0; +8.8] 6.7 785 107-70.0[-99.7; +105.8]10.3 803 0 GBM 6.5 -87.4 [-100.0; -30.8] 2.3 89.7 2 6.2 -85.2 [-100.0; -8.2] 1.8 87.0 3 GLM 166 -55.9 [-100.0; +67.9] 17.7 73.6 1 152 -57.3 [-99.9; +60.7] 19.8 77.1 0 MARS 36.1 +15.1 [-99.0; +449.3] 69.7 54.6 0 40.6 +21.3 [-99.6; +600.0] 69.8 48.4 0 MDA -10.8 [-89.7; +151.3] 57.4 0 19.9 -40.8 [-88.1; +19.2] 13.1 53.9 28.6 46.7 0

26.8

0

59.9

Mean prevalence of species in each model in 2051–2080, mean proportion of new squares occupied (Gain) and that of squares lost (Loss) with proportion of change (%), and no. of species becoming extinct based on climate-only variables and climate-topography variables in the two scenarios (A2, B1) between 1971–90 and 2051–2080. In brackets range of percent change in each of the models showing the between-species variation in net change.

Change is the mean proportional change of species distributions. Change = Gain - Loss.

-4.1 [-98.0; +170.0]

55.8

which often also means extrapolating the models into non-analogous climate conditions (Fitzpatrick and Hargrove, 2009). When present-day climate and future climate conditions differ markedly, all modelling techniques may face difficulties and produce biased projections (see Elith and Graham, 2009; Kühn et al., 2009). In the case of RF and GBM, this is because they are based on classification and regression trees that always extrapolate at a constant value from the last most extreme environmental value in the training data (Elith and Graham, 2009). This behavior may make them sensitive to the aberrant values at the margins of the speciesclimate space, e.g. resulting from insufficient field surveys or inaccurate recording of environmental parameters.

GAMs have been reported to perform rather well in several recent model comparison studies (e.g. Segurado and Araújo, 2004; Austin et al., 2006; Heikkinen et al., 2007; Meynard and Quinn, 2007), being generally inferior only to techniques such as GBM and RF (e.g. Guisan et al., 2007). In the present study, GAM performed very well, as it had on average the second highest splitsample evaluation AUC values and the highest species numbers with excellent AUC performance among the climate-topography models. Moreover, the mean projected changes in the species ranges (as regards prevalence, and change, gain and loss in the suitable climate space) provided by GAM were very similar to those provided by GBM and ANN. With respect to extrapolating the calibrated models into future climate scenarios, GAM may be expected to provide robust projections in cases where speciesclimate response surfaces are predominantly smooth. This is because GAMs are based on continuous curves, which may make these models easier to adopt into new areas or time periods (Thuiller et al., 2003).

Some recent studies have reported that MARS may also achieve a high prediction success, and have distinct advantages (e.g. due to its superior speed) for the analysis of large data sets (Leathwick et al., 2006; Elith and Leathwick, 2007). However, our results give little support to these conclusions. Most importantly, MARS, partly together with MDA, showed the greatest deviances from the general pattern in the model outputs. MARS was the only method that predicted a downward pattern in the altitude of the 5% species hotspots in both climate-only and climate-topography variables, and was also the only model predicting increase in species prevalence in both variable settings in both scenarios. In a similar vein, Prasad et al. (2006) concluded that MARS performs less well than techniques such as RF, and it may provide unrealistic projections when the models are transferred to future climate conditions. This is because MARS is highly sensitive to extrapolation, due to the local nature of the basic species-climate response functions (see Prasad et al., 2006).

62.7

+10.0 [-81.2; +246.1]

Recent papers have advocated the use of combinations of projections from multiple models (i.e consensus or ensemble modelling) in order to obtain more reliable forecasts of the potential range changes of the species (Araújo and New, 2007; Marmion et al., 2009a). However, instead of ensemble modelling we focused here on evaluating the agreements and dissimilarities among the outputs of the eight modelling techniques. This was because one of the limitations in ensemble modelling, i.e. deciding how many and which of the models should be combined, was apparent in our results. Algar et al. (2009) concluded that when a single-best model can be identified, incorporation of other models will bias the final projection away from the best model's predictions. Moreover, Araújo et al. (2005a) argued that there is no advantage in combining inferior forecasts with more accurate models, particularly if they deviate much from the general trends in predictions. In our case, combining the divergent projections from MARS and MDA (possibly resulting from their sensitivity to the challenges in extrapolation) with other models to produce consensus predictions would very probably bias the predictions of the more accurate methods. Visual examination of the direction of the projected range changes shows that predictions from ANN, CTA, GAM, GBM, and RF are often in good agreement. As RF, GBM and GAM also provided the best model accuracy, we conclude that the parallel results from these methods provide the most plausible forecasts for the studied species responses to future climate.

Bird species that showed the highest cross-validation AUC values were species from the harshest open alpine habitats, such as snow bunting *Plectrophenax nivalis*, long-tailed skua *Stercorarius longicaudus* and rock ptarmigan *Lagopus muta*, followed by bar-tailed godwit *Limosa lapponica* and red-throated pipit *Anthus cervinus* which favor northern palsa mires. Species with the most inaccurate models included four forest-dwelling species, two owl species (great grey owl and hawk owl) and two passerines

0

52.8



Fig. 3. Predicted distribution (A2 climate scenario for 2051–80) of rustic bunting *Emberiza rustica* (A, B) and that of brambling *Fringilla montifringilla* (C, D) based on climate-only (A, C) and climate-topography (B, D) variables. The prediction for rustic bunting is based on GBM and for brambling on GAM.

(Arctic warbler and two-barred crossbill). As regards species characteristics, the better predicted species had higher environmental specialization and more narrow and spatially agglomerated ranges, which is in agreement with recent studies on the impacts of species characteristics on the model performance (e.g. Luoto et al., 2005; Seoane et al., 2005; Guisan et al., 2007; McPherson and Jetz, 2007; Marmion et al., 2009b; Pöyry et al., 2008). McPherson and Jetz (2007) showed that model accuracy

can be lower in migratory bird species than in non-migrants. However, this was not apparent in our results, in which both the least accurately and best accurately modeled bird species included migratory as well as non-migratory species (Appendices A, B and C).

The bird species with the least accurate models were certain forest birds which are rather scarce in northern boreal and subarctic landscapes. This makes them unlikely to be modeled



Fig. 4. The mean change in location of 5% species number hotspots of cells from 1971–90 to 2051–80 (A2 climate scenario) in the eight models based on climate-only and climate-topography variables. N, E, S and W axes (in km) point toward cardinal points and down-up toward the altitude (in m).

with great accuracy (cf. Seoane et al., 2005). However, the speciesenvironment relationships and the accuracy of the models based on them also depend heavily on the spatial scale of observation (Vaughan and Ormerod, 2003; Guisan et al., 2007; Heikkinen et al, 2007), including bioclimatic envelope models and their projections (Luoto et al., 2007; Trivedi et al., 2008). Such scale-dependence probably affected our results, as was indicated by a comparison with the performance of bioclimatic envelope models in the recent Climatic Atlas of European Breeding Birds (Huntley et al., 2007). For example, all the four species that in our study were modeled with only moderate accuracy (great grey owl, hawk owl, Arctic warbler and two-barred crossbill; all with AUC < 0.75 in both climate-only and climate-topography models) were modeled in the Climatic Atlas with high accuracy (AUC > 0.98 for all four species). The Climatic Atlas is based on European-wide climate and bird data, which partly contributes to these differences between the two studies. However, spatial resolution (grain size) no doubt also affects the model performance. This is because the distribution patterns of the northern birds at the resolution of ca. 50 km used in the Climatic Atlas generally look spatially clumped and compact (see Huntley et al., 2007). By contrast, at the resolution of this study (10×10 min grid) the distribution of several species (e.g. the four example species) starts to look more sporadic, due to their scarcity in the landscape, inconspicuousness, or increasing impacts of other factors determining their distribution (see Pearson et al., 2004; Luoto et al., 2007; Trivedi et al., 2008).

The study by Marmion et al. (2009a) provides an option to compare the present results with results for another species group modeled at finer resolution in the northern boreal landscape.

Table 4

Mean proportion (%) of protected areas in the 5% hotspots of species numbers in the different models based on climate-only and climate-topography variables.

	Climate-only	y		Climate-top	graphy			
	1971-90	2051-8	0	1971-90	2051-80			
		A2	B1		A2	B1		
ANN	54.8	49.9.	50.1	46.3	43.4	42.8		
CTA	46.6	47.3	42.2	38.5	48.1	41.8		
GAM	56.6	50.0	45.2	50.6	42.9	40.8		
GBM	51.7	49.2	41.5	40.1	44.0	37.6		
GLM	56.1	30.2	47.4	53.4	45.6	39.7		
MARS	55.6	13.9	16.5	24.1	14.4	38.7		
MDA	37.7	22.6	22.5	46.3	24.4	18.1		
RF	37.0	49.5	46.5	31.2	45.7	52.4		
Mean	49.5	39.1	39.0	41.3	38.6	39.0		

Marmion et al. (2009a) compared the performance of the same eight modelling methods in analyzing the spatial distribution of 28 threatened plant species using data recorded at a resolution of 25 ha. In their analyses, one third of the species received poor values in the AUC (<0.7, 30.8%), in contrast to our 2.7% (12/448) of poor AUC-values in single models. These notable differences suggest that in finer-resolution studies species distributions are related to several other factors than just climate, whereas broad-scale macroecological patterns in bird distributions can be effectively captured by climatic variables (Huntley et al., 2007, 2008; Luoto et al., 2007).

Our results suggest that it may be fruitful to model the potential response of species to climate change with several modelling techniques, and then seek concordant patterns in the projected range changes that emerge from several models. This practice may help in identifying the most plausible forecasts for species under climate change scenarios, as well as excluding potentially dubious extrapolations, such as projections by one modelling technique consistently contradicting others. As regards modelling techniques themselves, our results suggest that RF, GBM, ANN and GAM have the potential to provide accurate models more often than the other methods used here. However, their results should also be treated with caution, not least because the performance of any modelling technique is dependent on many factors, including not only species characteristics and scale, but also several other sources of uncertainty (see Vaughan and Ormerod, 2003; Heikkinen et al., 2006).

4.2. Topographical heterogeneity

Our results indicate that including topographical variables has the potential to increase the accuracy of species-climate-only models in several of the modelling techniques employed here (statistically significantly in GAM, GLM and RF), and that climatetopography models on average estimate less net loss in species distributional area than climate-only models. Similar trends were apparent in the results of Luoto and Heikkinen (2008), in which the inclusion of topography caused even more notable improvements in the model performance. This difference was probably caused by the differences in the grain size between the two studies, as well as the fact that much more mountainous areas were included in the study by Luoto and Heikkinen (2008; see also Randin et al., 2009).

The variable employed in our study was one of the most basic measures used to describe topographical heterogeneity, namely elevation range. Elevation range has been commonly used as a surrogate for environmental and climatic heterogeneity within grid cells in species richness modelling studies (e.g. Richerson and Lum, 1980; Currie, 1991), based on a finding that topographical heterogeneity facilitates the compression of biotic communities into more constricted vertical spaces and supports the mingling of species that are otherwise often widely spatially separated (Coblentz and Riitters, 2004). In ecological terms, topography acts as an approximate surrogate of land cover or habitat heterogeneity in the predictions, and thus its inclusion in bioclimatic envelope modelling provides a means to capture part of the environmental variation within the 10' grid cells which would otherwise be lost in the climate values averaged over the whole grid cell (Luoto and Heikkinen, 2008).

The problem of heterogeneity within grid cells has been taken more into consideration in bioclimatic envelope modelling only recently, although the argument that areas in heterogeneous terrain may enhance the persistence of biodiversity under changing climate was put forward already by Peters and Darling (1985). Peterson (2003) compared the outputs from bioclimatic models for simulated bird species distributions in Great Plains vs. Rocky Mountains. This study showed that species of flatland areas appear to be more heavily influenced by climate change and may face more drastic area reductions than species inhabiting topographically heterogeneous areas. Luoto and Heikkinen (2008) specifically incorporated the within-cell elevation heterogeneity in bioclimatic models, and reported that accounting for heterogeneity may decrease the estimated extinction risk for species in mountainous landscapes. By contrast, based on a comparison of the outputs from bioclimatic models at different spatial scales, Trivedi et al. (2008) showed that fine resolution local-scale models may estimate more drastic loss of suitable climate space in mountain species than coarse resolution macro-scale models. Trivedi et al. (2008) concluded that coarse-scale European models may overestimate the thermal tolerances of species and thus overestimate both the present distributions of mountain species and their ability to cope with increasing temperatures [see also Sekercioglu et al. (2008)].

These contrasting findings are probably caused by the differences in the types of species used in the studies. Trivedi et al. (2008) based their conclusions on cold-adapted mountain plant species which apparently already presently occur in the coldest places within the coarse-resolution grid cells. Such species may in reality be more sensitive to climate warming than was estimated by coarse-scale bioclimatic models, especially if they occur in gently sloping mountain regions with only a limited amount of high alpine habitats. By contrast, the study of Peterson (2003) did not include any highest-mountain species and in Luoto and Heikkinen (2008) only 10% of the species were mountain species. Large within-cell elevation heterogeneity may significantly decrease the local extinction risk for the species inhabiting foothills and lower-middle elevations by enhancing the ability of such species to track the spatial changes in their climate optima due to shorter dispersal distances (Guralnick, 2006). Interestingly, Randin et al. (2009) reached conclusions contrasting those of Trivedi et al. (2008) and reported that European-wide model projections might overestimate extinction risks for alpine species. Further studies are required to assess the reasons for these discrepancies, but one possible underlying factor is the notable difference in the magnitude of the elevation range and the degree of ruggedness between the study areas.

There are apparently several different ways to take topographical heterogeneity into account in bioclimatic modelling. However, a take-home message of this study and other recent studies (Peterson, 2003; Luoto and Heikkinen, 2008; Trivedi et al., 2008; Ashcroft et al., 2009; Randin et al., 2009) is that in mountainous areas topographical heterogeneity should be incorporated into predictions of how species will respond to climate change, because models using coarse-grained climate surfaces may critically underestimate or overestimate the ability of species to cope with projected warming. Outputs from the modelling studies that have not taken within-cell heterogeneity into account should thus be interpreted with caution in mountainous areas (Thuiller et al., 2005b; Luoto and Heikkinen, 2008).

4.3. Conservation implications

The ability to simulate the potential changes in the distribution range in northern land birds as accurately as possible is also important from the point of view of nature conservation. Northern boreal habitats are highly important for conservation of birds, but apparently are also very susceptible to climate change. For example, in northernmost Europe wet, structurally diverse palsa mires created by permafrost are expected to decline and become more homogeneous during the next 50 years as a consequence of climate warming, resulting in decreased abundances of bird populations inhabiting these ecosystems (Luoto et al., 2004). Palsa mires, situated mostly in our 5% hotspots of species diversity, are highly valuable for northern bird species: for example, of 11 biotopes in Finnish Lapland, the density and species richness of both passerines and waders were highest in palsa mires, being more than double that of the second highest value from alpine peatlands (Järvinen and Väisänen, 1976). Of the species included in the present study, bar-tailed godwit breeds almost exclusively in palsa mires and several other species, including red-necked phalarope (Phalaropus lobatus), Lapland longspur (Calcarius lapponicus) and red-throated pipit clearly prefer this habitat type. In the whole of northwestern Europe (Fennoscandia) the overall species richness of waders is highest in northernmost Finland and in Finnmark, probably due to the diversity of peatlands (Järvinen and Väisänen, 1978). Thus severe changes in the climatic suitability and the physiognomy of these palsa mire ecosystems may cause a decline in populations of bird species dwelling in these environments.

The coincidence of projected hotspots of the studied bird species and grid cells harboring large protected areas appears to decline clearly by 2051-80 on the basis of climate-only models and also slightly according to climate-topography models. These findings suggest that in the future, smaller proportions of populations of northern land birds will be included in the protected areas, although the protected area network should particularly preserve species declining due to climate change. It is particularly worrying that species are not predicted to concentrate in the grid cells with larger protected areas in the future. The probable decrease in significance of protected areas for northern-boreal birds may have important consequences for conservation planning in northern Europe, and thus there is an urgent need to investigate this issue in further detail (see Hannah et al., 2007; Huntley et al., 2008). The potential significance of such detailed analysis is emphasized by the fact that the Arctic Ocean represents an effective natural barrier to northward range shifts of the northernboreal land bird species (Virkkala et al., 2008). In a similar vein, the European-wide bioclimatic modelling study by Huntley et al. (2006) also showed that northern bird species will potentially become more restricted to high latitudes and/or altitudes in Europe. Moreover, these authors argued that common species of the extensive zone of broad-leaved forests have the potential to extend their ranges northwards at the expense of boreal and subarctic species.

From the point of view of the ecological requirements of individual species, protected areas are particularly important for the studied species because many of them have already declined due to direct human-caused habitat alteration, such as logging of oldgrowth coniferous forests and drainage of mires. Several species in our study, such as Siberian jay *Perisoreus infaustus*, Siberian tit *Parus cinctus*, and pine grosbeak *Pinicola enucleator*, prefer old-growth forests (Virkkala, 1991; Virkkala and Rajasärkkä, 2006). Mires have been drained particularly in southern Finland for forestry purposes, with a negative effect on the populations of mire birds such as the willow grouse *Lagopus lagopus* (Väisänen et al., 1998). Thus, human-caused habitat loss will accelerate the negative effects of projected climate change on these northern bird species, and the role of protected areas is likely to become even more important in the future.

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Appendix A

Prevalence (%), main habitats ($F =$ forest, $H =$ mountain heath, $M =$ mire) and migra-
tory status (M = migratory, R = resident or irruptive) of the studied 28 northern land
bird species, $N = 2655$ cells.

Species	Prevalence (%)	Main habitat	Migratory status
Rock ptarmigan Lagopus muta	6.7	Н	R
Willow grouse Lagopus lagopus	72.1	М	R
Rough-legged buzzard Buteo lagopus	35.5	F	М
Eurasian dotterel Charadrius morinellus	4.8	Н	М
Jack snipe Lymnocryptes minimus	20.2	М	М
Bar-tailed godwit Limosa lapponica	6.7	Μ	М
Whimbrel Numenius phaeopus	53.6	Μ	М
Spotted redshank Tringa erythropus	30.4	Μ	М
Common greenshank Tringa nebularia	68.1	Μ	М
Temminck's stint Calidris temminckii	12.9	Н	Μ
Broad-billed sandpiper	11.7	Μ	Μ
Limicola falcinellus			
Red-necked phalarope	22.7	Μ	Μ
Phalaropus lobatus			
Long-tailed skua Stercorarius	12.5	Н	M
longicaudus			
Great grey owl Strix nebulosa	12.4	F	R
Hawk owl Surnia ulula	32.6	F	R
Siberian jay Perisoreus infaustus	39.3	F	R
Bohemian waxwing Bombycilla garrulus	26.3	F	R
Siberian tit Parus cinctus	24.6	F	R
Horned lark Eremophila alpestris	1.2	Н	M
Arctic warbler Phylloscopus borealis	7.3	F	М
Red-throated pipit Anthus cervinus	9.1	Μ	М
Brambling Fringilla montifringilla	92.1	F	Μ
Pine grosbeak Pinicola enucleator	15.4	F	R
Two-barred crossbill Loxia leucoptera	10.1	F	R
Little bunting Emberiza pusilla	7.6	Μ	M
Rustic bunting Emberiza rustica	65.9	F	M
Lapland longspur Calcarius lapponicus	15.9	Μ	М
Snow bunting Plectrophenax nivalis	7.8	Н	М

Appendix C (continued)

Appendix B

The Area Under Curve (AUC) values for the 28 northern land birds in Finland-Finnmark from the 70:30 split-sample evaluation. The modelling is based on four climatic variables only and includes 8 modelling techniques: artificial neural networks (ANN), classification tree analysis (CTA), generalized additive models, generalized boosting method (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), mixture discriminant analysis (MDA), and random forest (RF). Mean AUC = mean AUC averaged over the 8 models.

	ANN	CTA	GAM	GBM	GLM	MARS	MDA	RF	Mean
	AUC								
Lagopus lagopus	0.827	0.818	0.843	0.839	0.834	0.815	0.795	0.880	0.831
Lagopus muta	0.902	0.900	0.901	0.864	0.908	0.868	0.901	0.898	0.893
Buteo lagopus	0.887	0.883	0.877	0.886	0.874	0.876	0.868	0.893	0.881
Charadrius morinellus	0.878	0.863	0.874	0.870	0.866	0.822	0.763	0.858	0.849
Lymnocryptes minimus	0.748	0.728	0.723	0.736	0.705	0.741	0.689	0.775	0.731
Limosa lapponica	0.923	0.885	0.901	0.900	0.895	0.800	0.819	0.926	0.881
Numenius phaeopus	0.840	0.817	0.826	0.824	0.828	0.831	0.820	0.847	0.829
Tringa erythropus	0.858	0.794	0.843	0.844	0.842	0.846	0.825	0.861	0.839
Tringa nebularia	0.819	0.817	0.823	0.814	0.817	0.823	0.772	0.844	0.816
Calidris temminckii	0.860	0.837	0.857	0.853	0.853	0.840	0.846	0.863	0.851
Limicola falcinellus	0.810	0.785	0.776	0.780	0.757	0.783	0.784	0.802	0.785
Phalaropus lobatus	0.830	0.825	0.822	0.833	0.818	0.835	0.815	0.842	0.828
Stercorarius	0.952	0.944	0.960	0.954	0.954	0.959	0.935	0.955	0.952
longicaudus									
Strix nebulosa	0.779	0.742	0.744	0.744	0.750	0.749	0.709	0.720	0.742
Surnia ulula	0.725	0.715	0.715	0.724	0.717	0.733	0.693	0.749	0.721
Perisoreus infaustus	0.822	0.811	0.826	0.826	0.816	0.828	0.805	0.863	0.825
Bombycilla garrulus	0.808	0.804	0.784	0.786	0.770	0.788	0.775	0.803	0.790
Parus cinctus	0.912	0.888	0.914	0.903	0.890	0.901	0.885	0.909	0.900
Eremophila alpestris	0.880	0.856	0.850	0.900	0.891	0.924	0.715	0.923	0.867
Phylloscopus borealis	0.718	0.674	0.763	0.763	0.732	0.737	0.747	0.703	0.730
Anthus cervinus	0.901	0.839	0.894	0.881	0.884	0.868	0.860	0.884	0.876
Fringilla montifringilla	0.817	0.741	0.827	0.808	0.819	0.778	0.751	0.820	0.795
Pinicola enucleator	0.863	0.866	0.855	0.863	0.854	0.850	0.846	0.852	0.856
Loxia leucoptera	0.780	0.652	0.719	0.726	0.716	0.733	0.719	0.729	0.722
Emberiza pusilla	0.829	0.837	0.857	0.850	0.847	0.854	0.895	0.820	0.849
Emberiza rustica	0.832	0.810	0.803	0.812	0.793	0.785	0.805	0.855	0.812
Calcarius lapponicus	0.931	0.925	0.922	0.924	0.928	0.932	0.914	0.909	0.923
Plectrophenax	0.917	0.903	0.919	0.896	0.909	0.920	0.912	0.891	0.908
nivalis									

Appendix C

The Area Under Curve (AUC) values for the 28 northern land birds in Finland-Finnmark from the 70:30 split-sample evaluation. The modelling is based on four climatic variables and elevation range and includes 8 modelling techniques: artificial neural networks (ANN), classification tree analysis (CTA), generalized additive models, generalized boosting method (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), mixture discriminant analysis (MDA), and random forest (RF). Mean AUC = mean AUC averaged over the 8 models.

	ANN	CTA	GAM	GBM	GLM	MARS	MDA	RF	Mean
	AUC								
Lagopus muta	0.904	0.905	0.923	0.913	0.922	0.902	0.919	0.914	0.913
Lagopus lagopus	0.819	0.818	0.832	0.842	0.830	0.849	0.742	0.877	0.826
Buteo lagopus	0.885	0.883	0.877	0.887	0.874	0.876	0.854	0.891	0.878
Charadrius morinellus	0.924	0.861	0.909	0.861	0.907	0.895	0.877	0.883	0.890
Lymnocryptes minimus	0.752	0.771	0.759	0.764	0.757	0.743	0.735	0.785	0.758
Limosa lapponica	0.915	0.902	0.912	0.900	0.907	0.882	0.876	0.917	0.901
Numenius phaeopus	0.830	0.817	0.830	0.828	0.830	0.835	0.810	0.852	0.829
Tringa erythropus	0.854	0.835	0.852	0.857	0.856	0.866	0.820	0.863	0.849
Tringa nebularia	0.799	0.817	0.825	0.823	0.825	0.823	0.758	0.836	0.813
Calidris temminckii	0.840	0.868	0.863	0.850	0.862	0.815	0.862	0.871	0.854
Limicola falcinellus	0.859	0.766	0.818	0.790	0.795	0.797	0.745	0.813	0.798
Phalaropus lobatus	0.829	0.827	0.823	0.834	0.813	0.851	0.800	0.847	0.828
Stercorarius longicaudus	0.963	0.944	0.960	0.954	0.960	0.955	0.948	0.956	0.955
Strix nebulosa	0.770	0.764	0.742	0.747	0.739	0.697	0.700	0.705	0.733

	ANN	CTA	GAM	GBM	GLM	MARS	MDA	RF	Mean
	AUC								
Surnia ulula	0.704	0.695	0.723	0.719	0.709	0.719	0.695	0.752	0.715
Perisoreus infaustus	0.824	0.807	0.826	0.826	0.816	0.825	0.805	0.863	0.824
Bombycilla garrulus	0.773	0.783	0.797	0.793	0.784	0.794	0.762	0.803	0.786
Parus cinctus	0.889	0.888	0.905	0.895	0.901	0.888	0.865	0.912	0.893
Eremophila alpestris	0.909	0.885	0.919	0.900	0.917	0.725	0.908	0.979	0.893
Phylloscopus borealis	0.653	0.674	0.745	0.752	0.737	0.746	0.703	0.722	0.717
Anthus cervinus	0.914	0.861	0.911	0.890	0.906	0.905	0.899	0.903	0.899
Fringilla montifringilla	0.817	0.661	0.818	0.800	0.815	0.698	0.727	0.820	0.770
Pinicola enucleator	0.859	0.862	0.859	0.864	0.863	0.858	0.847	0.868	0.860
Loxia leucoptera	0.764	0.652	0.738	0.720	0.725	0.729	0.722	0.743	0.724
Emberiza pusilla	0.853	0.837	0.857	0.858	0.847	0.721	0.821	0.833	0.828
Emberiza rustica	0.820	0.808	0.806	0.809	0.794	0.816	0.741	0.869	0.808
Calcarius lapponicus	0.925	0.904	0.923	0.926	0.925	0.934	0.914	0.928	0.922
Plectrophenax nivalis	0.913	0.903	0.922	0.905	0.934	0.929	0.915	0.929	0.919

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