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Projected large-scale range reductions of northern-boreal land bird species due to climate change

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ABSTRACT

Climate change is projected to be particularly strong in the northern latitudes. Thus, boreal or arctic species are especially susceptible to the effects of climate warming. In this work we forecasted changes in the distributions of 27 northern land bird species in the 21st century, based on predicted rates of climate change. We used climate and bird atlas data of Finland and northern Norway from 1971–1990 to establish bioclimatic envelope models for each species. Next, these models were applied to two climate scenarios (A2 and B1) from the general circulation model HadCM3 to forecast potential future distributions of the study species over a larger area also covering parts of nearby Sweden and Russia. This area stretches through the boreal and continental arctic zone in northern Europe. In the A2 scenario the predicted global change in mean temperature is 3.8 °C by 2100 and in the B1 scenario 2.0 °C. Our results suggest that most of the northern land bird species will lose most of their climatic space by 2080 both in the more severe (A2, average predicted range decline: –83.6%) and in the less severe scenario (B1, average change: –73.6%). A large proportion (over two thirds) of the species considered here is thus susceptible to major range contractions in this geographical region. These climate change-induced threats are of importance because the Arctic Ocean represents a natural barrier for northward movement of species. To reduce the negative effects of climate change on the northern species, relatively large areas of continuous habitats in a connected reserve network should be preserved.

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1. Introduction

Climate change is one of the most important threats to biodiversity (Parmesan and Yohe, 2003; Root et al., 2003). Species are expected to react to climate change in various ways. Typical patterns include range shifts (Parmesan et al., 1999; Thomas and Lennon, 1999; Thomas et al., 2006), changes in phenology (breeding and migration patterns of birds) (Crick et al., 1997; Jonzén et al., 2006) and physiological adaptations

to changing climate (Jiguet et al., 2006). Phenotypic adaptation can facilitate species persistence in a given site in a changing climate (Schaefer et al., 2008). In general, climate affects species both directly and indirectly. Direct impacts include high or low temperatures above or below which a species cannot survive (for northern birds, see Root, 1988). Indirect effects include particularly latitudinal or altitudinal change in the habitat preferred by the species and changes in habitat structure and quality. Such habitat-based changes may often result in

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increased effects of habitat fragmentation due to human activities (Honnay et al., 2002; Opdam and Wascher, 2004).

In both historical and geological time scales species extinctions caused by climate change have been common. For example, the large-scale extinctions of megafauna between 50,000 and 10,000 years BP with varying time periods in the continents of Australia, South and North America and Eurasia were at least partly caused by climate change (Stuart, 1991; Barnosky et al., 2004). The ongoing climate change is expected to cause species extinctions in significant numbers (Thomas et al., 2004). The rate of the future extinctions caused by rapid climate change will be further accelerated by the fact that nowadays habitats are fragmented due to human land use and therefore species cannot shift their ranges as easily as in prehistoric times (Huntley, 1998; Travis, 2003; Pearson and Dawson, 2005).

The predicted increase in temperature is likely to be particularly dramatic in the northern latitudes (IPCC, 2001). Therefore, species especially susceptible to the effects of climate warming are those concentrated in their distribution in the northern-boreal or arctic zones. In a recent study of global diversity of birds, climate change-induced land cover changes were projected to have the greatest impact on species far from the equator, particularly in the northern landmasses, whereas direct anthropogenic land conversion was the most significant threat in the tropics (Jetz et al., 2007).

On a broad spatial scale climate variables have been observed to be good predictors of species distribution (Huntley et al., 2004, 2006; Pearson et al., 2004; Ellis et al., 2007). Based on such findings, bioclimatic envelope models are increasingly used to examine relationships between climate variables and species distributions. Using these models present climate is related to present species ranges and spatial distribution. Possible decrease of suitable future climate space for species can then be predicted based on different climate scenarios for a given geographical area (Heikkinen et al., 2006 and references therein). For example, in a study of 1200 European vascular plant species, 5% of the species were predicted to lose their entire bioclimatic envelope in Europe by 2021–50 based on a severe climate scenario (Araújo et al., 2004).

In this work we used bioclimatic envelope modeling to predict changes in the distributions of 27 land bird species in the 21st century, based on current predicted rates of climate change. The studied species breed in boreal forests, in mires, and in mountain heaths with vegetation similar to tundra. All these habitat types are expected to change considerably in the future (Skre et al., 2002).

The study was carried out in Fennoscandia: in Finland and in adjoining regions in Norway, Sweden, and Russia. This study area stretches through the boreal and continental arctic zone in northern Europe. Because latitudinal vegetation zones are expected to move northwards, species occurring in the boreal and continental arctic zones will be limited in their range expansion by the Arctic Ocean. Therefore, study of the predicted distribution patterns of northern-boreal species based on their climate space is of significant importance in evaluating the effects of climate change on global biodiversity.

2. 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) in developing 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 Gulf of Finland (Baltic Sea) to the Arctic Ocean, between 59°50' N and 71°5' N and between 20°35' and 31°35' E, and included in total approximately 350 000 km² of land area. In the second stage of the modeling, we applied the bioclimatic models developed for the study 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 (see Fig. 1B). The rationale for this was that boreal areas ecologically very similar to our core study area continue from Finland and Finnmark to the west in Sweden and in Norway and to the east in Russia.

The climate of Finland and Finnmark shows characteristics of both oceanic and continental climates and is subject to Atlantic, Arctic and Siberian influences, the continentality growing inland and eastwards (Tuhkanen, 1984). The majority 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 subarctic region in northernmost Finland (Lapland) and 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.

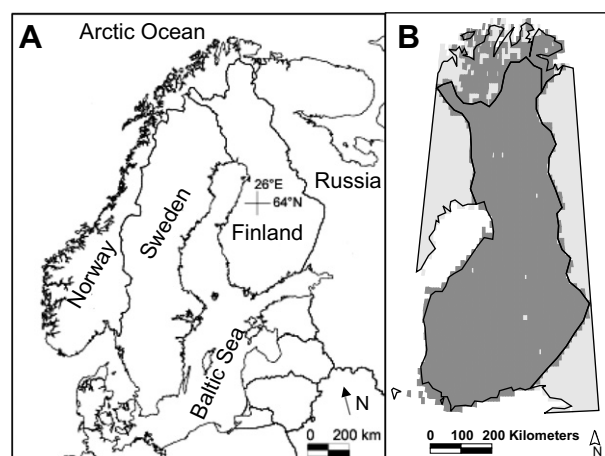


Fig. 1 – A. Location of Fennoscandia (Norway, Sweden, Finland and NW Russia) in north-western Europe. B. 10' × 10' grid cells with atlas data used in Finland and Finnmark ($n = 2655$; i.e. the core study area used in model building shown with darker grey) and the larger region (lighter grey) to which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

Biogeographically Finland stretches through the boreal coniferous vegetation zone, where there are only two dominating coniferous tree species, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Ahti et al., 1968). The northern forest boundary of spruce is in northernmost Finland (northern Lapland) and that of pine 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. Open wet mires, such as aapa fens and palsa mires are highly important for several wader species (Väisänen et al., 1998). In northernmost Finland and in Finnmark there are mainly gently sloping mountains with treeless heath vegetation.

2.2. Bird data

We included 27 land bird species in our analyses: 10 species were breeding and/or foraging primarily in forests, 11 in mires, and 6 in mountain heaths (Table 1). Eighteen 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). However, the rock ptarmigan (*Lagopus muta*) breeding in mountain heaths, also has separate populations in the Alps, the Pyrenees and Scotland. In the case of the horned lark (*Eremophila*

alpestris), the subspecies *E. a. flava* breeds in northern Europe and *E. a. balcanica* in the Balkans and Greece (Hagemeijer and Blair, 1997).

We used the pooled information of two bird atlas surveys carried out in Finland: field work for the first was performed in 1974–79 and that for the second in 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 included in the data. Both the Finnish and north Norwegian atlases used 10 × 10 km grids, in which observations of species were recorded.

The breeding status of bird species recorded in each of the grid squares were listed in four classes: 0 = not found, 1 = breeding possible (e.g. singing or displaying male observed once in a typical nesting habitat), 2 = breeding probable (e.g. singing or displaying male with a persistent territory observed, or female or pair present on more than 1 day in the same place, or bird observed building a nest), 3 = confirmed breeding (Väisänen, 1989). For the analyses of this study, we combined classes 1, 2 and 3 as a species presence-variable (see Virkkala et al., 2005). In Finland, where over 90% of the grid cells were situated in our data, the atlas surveys graded the survey activity in each square according to six categories: 0 = no observations, 1 = occasional observations, 2 = fair surveys, 3 = satisfactory survey of the square, 4 = well surveyed and 5 = thoroughly surveyed squares (Väisänen et al., 1998).

Table 1 – Prevalence, explained deviance of the GAM models, and AUC (based on cross-validation) of the studied 27 northern land bird species, N = 2655 cells

Species	Prevalence (%)	Deviance explained (%)	Drop contribution	AUC habitat	Main
Rock ptarmigan <i>Lagopus muta</i>	6.7	49.1	T_{AMJ}	0.944	H
Willow ptarmigan <i>Lagopus lagopus</i>	72.1	36.0	T_{AMJ}	0.868	M
Rough-legged buzzard <i>Buteo lagopus</i>	35.5	55.2	T_{AMJ}	0.937	F
Eurasian dotterel <i>Charadrius morinellus</i>	4.8	41.1	T_{AMJ}	0.920	H
Jack snipe <i>Limnospiza minimus</i>	20.2	21.4	P_{DJF}	0.802	M
Bar-tailed godwit <i>Limosa lapponica</i>	6.7	51.4	T_{AMJ}	0.950	M
Whimbrel <i>Numenius phaeopus</i>	53.6	41.2	T_{AMJ}	0.885	M
Spotted redshank <i>Tringa erythropus</i>	30.4	42.2	T_{AMJ}	0.901	M
Common greenshank <i>Tringa nebularia</i>	68.1	35.1	T_{AMJ}	0.861	M
Temminck's stint <i>Calidris temminckii</i>	12.9	41.3	T_{AMJ}	0.913	H
Broad-billed sandpiper <i>Limicola falcinellus</i>	11.7	26.9	T_{AMJ}	0.846	M
Red-necked phalarope <i>Phalaropus lobatus</i>	22.7	34.2	T_{AMJ}	0.873	M
Long-tailed skua <i>Stercorarius longicaudus</i>	12.5	70.3	T_{AMJ}	0.979	H
Great grey owl <i>Strix nebulosa</i>	12.4	19.7	T_{AMJ}	0.804	F
Hawk owl <i>Surnia ulula</i>	32.6	17.5	T_{AMJ}	0.769	F
Siberian jay <i>Perisoreus infaustus</i>	39.3	38.3	T_{AMJ}	0.952	F
Bohemian waxwing <i>Bombycilla garrulus</i>	26.3	30.2	T_{AMJ}	0.848	F
Siberian tit <i>Parus cinctus</i>	24.6	57.8	T_{AMJ}	0.952	F
Horned lark <i>Eremophila alpestris</i>	1.2	33.9	T_{AMJ}	0.899	H
Red-throated pipit <i>Anthus cervinus</i>	9.1	47.9	T_{AMJ}	0.940	M
Brambling <i>Fringilla montifringilla</i>	92.1	32.6	T_{AMJ}	0.819	F
Pine grosbeak <i>Pinicola enucleator</i>	15.4	50.8	T_{AMJ}	0.935	F
Two-barred crossbill <i>Loxia leucoptera</i>	10.1	16.6	T_{AMJ}	0.782	F
Little bunting <i>Emberiza pusilla</i>	7.6	34.2	T_{AMJ}	0.892	M
Rustic bunting <i>Emberiza rustica</i>	65.9	42.1	T_{AMJ}	0.861	F
Lapland longspur <i>Calcarius lapponicus</i>	15.9	59.2	T_{AMJ}	0.957	M
Snow bunting <i>Plectrophenax nivalis</i>	7.8	53.3	T_{AMJ}	0.951	H
Mean (\pm standard error)	26.6 \pm 4.6	40.0 \pm 2.6		0.888 \pm 0.011	

The most important explanatory variable based on drop contribution (highest residual deviance after excluding a variable from the final model): T_{AMJ} = mean temperature in April–June, P_{DJF} = precipitation in December–February. Main habitats of species: F = forest, H = mountain heath, M = mire.

We used grid squares with survey activity 2–5 in our analyses. In Finnmark no such classification of survey activity was available. However, to avoid squares with only occasional observations we took into account all squares, where any of the studied species were observed and squares with probable or confirmed breeding of any other species. Species data were eventually available from about 95% of all cells in our study area of Finland – Finnmark (Fig. 1B).

Because climate data in north-western Europe was available only for $10' \times 10'$ grids, the original bird records collated using the 10×10 km grids were transformed into the $10' \times 10'$ grid system. A cell in the $10' \times 10'$ grid was interpreted as occupied by a species when the original occupied 10 km grid cells covered at least 40% of the $10'$ cell.

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 most common species in the data was the brambling (*Fringilla montifringilla*), with a prevalence of 92.1%, and the rarest was the horned lark (prevalence 1.2%, Table 1). Mean prevalence of the 27 species was 25.9%.

2.3. Climate data

The climate data included mean values for the period 1971–1990 and predicted values for 2021–2050 and 2051–2080 for all climatic variables. We used climate data from the years 1971–1990 to build the bioclimatic envelope of each of the species, as it covers all the three atlas studies. 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 (T_{AMJ}), precipitation in April–June (P_{AMJ}), mean temperature of the coldest month (MT_{CO}) and precipitation in December–February (P_{DJF}) (see Forsman and Mönkkönen, 2003). The significance of each of these variables in explaining the distribution of the studied bird species in 1971–90 was studied in a statistical model (see statistical analyses) and the significant explanatory variables were used in building a bioclimatic envelope for each species.

We used observed and projected climate scenario data from the general circulation model HadCM3 General Circulation Model with a $10'$ resolution and two emission scenarios: B1 and A2 (Mitchell et al., 2004), 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 CO_2 is expected to increase from the present 380 parts per million (ppm) to 530 ppm and in A2 to 860 ppm by 2100. We used the mean values of climate variables for two time periods for the A2 scenario, 2021–2050 and 2051–2080, and the latter time period for the B1 scenario.

Of the six available emission scenarios (A1FI, A1B, A1T, A2, B1, B2), B1 is the most optimistic and A2 the second most severe scenario after A1FI (IPCC, 2001). In the northern latitudes (60° – 90°) the projected temperature increase is much higher than the global average. For example, based on the A2 scenario temperature increase in the Arctic is expected to be

7°C by 2100, with wide regional variation (ACIA, 2005). The A2 scenario was selected for the purposes of this study, instead of A1FI, for two pragmatic reasons: (i) for the sake of consistency and easier comparability with recent national studies; the majority of the study area belonged to Finland, and the recent climate scenarios generated by the FINADAPT ('Assessing the adaptive capacity of the Finnish environment and society under a changing climate'; Carter, 2007) research consortium also focused on the scenarios B1 and A2; (ii) the A1FI scenario data was available in the ALARM project as an up-scaled data, extrapolated from the A2 scenario data, whereas the A2 scenario data was available as the original data provided by the Hadley Center. Thus we opted here for circumventing one potential source of data uncertainty and preferred to use the original A2 data rather than the extrapolated A1FI data.

2.4. Statistical analyses

We used generalised additive models (GAMs) (Hastie and Tibshirani, 1990) in our analyses. GAMs were performed using GRASP (Generalised Regression Analysis and Spatial Prediction) in S-Plus (Version 6.1 for Windows, Insightful Corp.) (Lehmann et al., 2003). The GAMs were built using a stepwise selection procedure to select relevant explanatory variables and the level of complexity of the response shapes of the various species to each variable. A starting model including all continuous predictors smoothed with 4 degrees of freedom was fitted first. The variable dropping or conversion to linear form was then tested using Akaike's Information Criterion (AIC). Because the response variables represent binary data (presence or absence of species), a binomial distribution of error via a logistic link function was applied as suggested by Lehmann et al. (2003).

We evaluated the models based on the explained deviance (%) and assessed the discrimination ability (performance) of the predictive 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.

The original data of species presence were extrapolated to a larger region, including areas in northern Sweden, northern Norway and in north-western Russia connected to the core study area for the periods 1971–90, 2021–2050 and 2051–2080 (Fig. 1B). This area of predicted presence of species covered a uniform area of 3901 grid cells. The model calculated probability of occurrence in a cell for each species. When converting the probability values into presence–absence records of species in a cell, a cut-off based on the original prevalence of species was used. Thus, for example, if the original prevalence of a species had been e.g. 20%, then the cut-off value of the probability of presence in the predicted data sets would also be 20% (Liu et al., 2005).

We measured the modeled distribution of species based on climate suitability. We compared the predicted species distributions in 1971–1990 to those in 2021–2050 and 2051–2080. The approaches developed by Ohlemüller et al. (2006a, b) were then adopted in order to carry out the following comparisons:

- (1) Change in climatically suitable area. We calculated the climatically suitable area for each species in each period based on predicted presence-absence. Prevalence of species was used as a threshold for presence-absence (see Liu et al., 2005). The sums of climatically suitable areas (species present) were compared (subtracted) between the latter periods and the period of 1971–1990 (predicted distribution) so that higher negative values in percentage change indicated higher loss of climatically suitable area.
- (2) Change in distance to the nearest climatically suitable cell. The distance of a climatically suitable cell to the nearest climatically suitable cell in 1971–1990 (predicted distribution) was recorded, and the distances between climatically suitable cells in the latter periods and in 1971–1990 were calculated. The distance from the latter period was subtracted from the distance in 1971–1990. High values represent increasing distance to the future climatically suitable cell.
- (3) Change in average climatic suitability of already occupied cells. Here we used only the 2655 grid cells included in the original atlas data (see Fig. 1B). We studied how much average probability of occurrence (i.e. predicted climatic suitability) for each species, based on the prediction in 1971–1990 in the occupied cells, would change in the latter periods. This was done simply by comparing the probabilities of occurrence for each species in 1971–1990 in each occupied cell with the probabilities of occurrence in the same cells in the later time periods, generated by applying the bioclimatic models to the different scenario data.

3. Results

In general, under the predicted climate change scenarios the results of this study are rather straightforward: over 70% of the northern bird species were projected to lose over 60% of their climatic space by 2080 both in the more severe (A2) and in the less severe scenario (B1). This means that over two thirds (over 20) of the species considered here are susceptible to major range contractions in this geographical region cross-cutting the boreal and continental arctic zones.

Bioclimatic models explained on average 40% of deviance in GAM models of the 27 species (variation between species 16.6–59.2%, Table 1). The most important climate variable based on drop contribution was the mean temperature in April–June for all but one species. Accuracy in values of AUC was good (between 0.8 and 0.9) or excellent (over 0.9) for 25 out of 27 species. Correlation between prevalence and AUC was slightly, but non-significantly negative ($r = -0.340$, $p = 0.082$, $n = 27$), whereas there was no correlation between prevalence and deviance explained ($r = -0.133$, $p = 0.509$).

Predicted species numbers were highest (>20 species) in northernmost Finland and in parts of northern Sweden and Norway and in north-western Russia in 1971–1990 (Fig 2). Based on scenario A2, species numbers were projected to be highest (over 13 species) in northernmost Sweden in 2051–2080, and the greatest species losses would occur in northernmost and northeastern Finland (Fig. 2).

Climatically suitable area for the species declined on average 57.6% by 2021–50 and 83.6% by 2051–2080 based on the scenario A2 (Table 2, Fig. 3). In the scenario B1 climatically suitable area of the 27 species declined on average 73.6% by

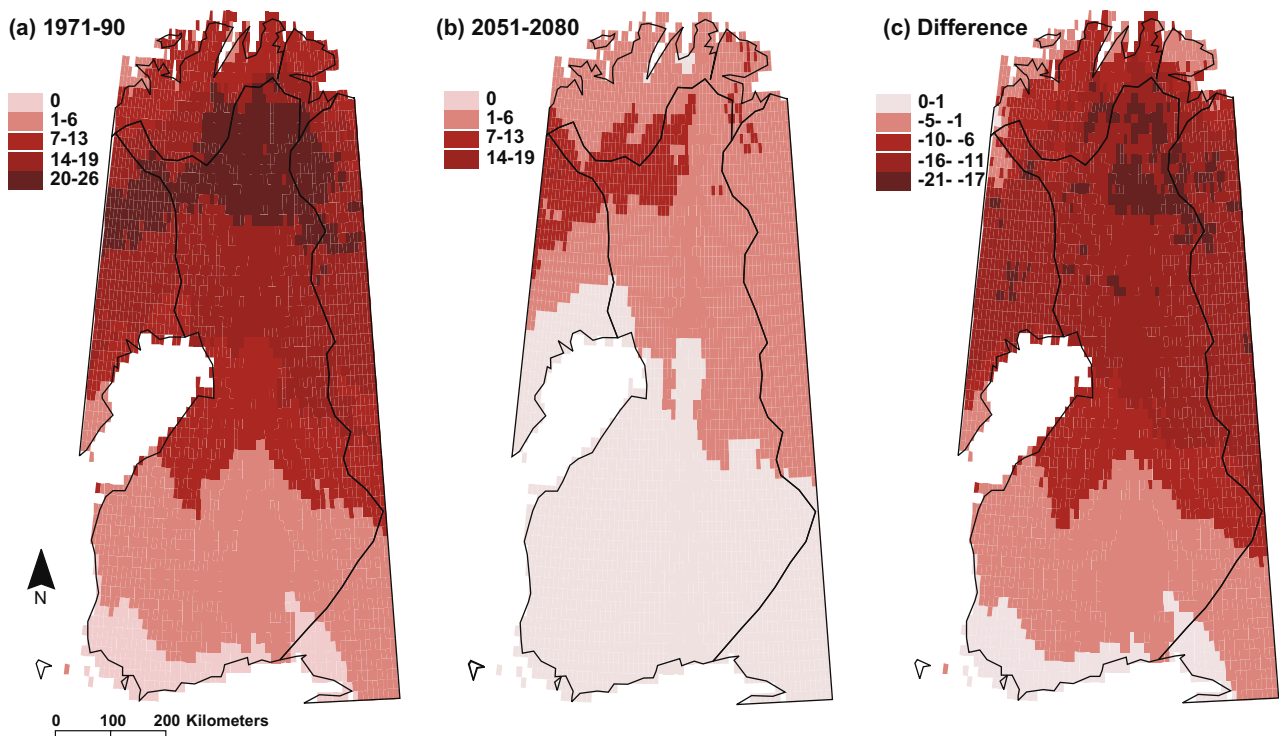


Fig. 2 – Predicted bird species numbers of the 27 northern bird species in 1971–1990 (a), in 2051–2080 (b) based on climate scenario A2 and the difference (c) in the predicted species numbers between 1971–1990 and 2051–2080 in the 10' grid scale in Finland, northern Norway, northern Sweden and north-western Russia based on bioclimatic envelope modeling.

Table 2 – Results of the modeled distribution of the 27 northern land bird species. Change in distribution shows the percentage change between the predicted 1971–1990 distribution and that of the latter period(s) based on scenarios A2 and B1 (see text)

Species	Change in distribution (%)			Change in distance to nearest climatically suitable cell (km)			Change in probability of cells already occupied		
	A2 2021–50	A2 2051–80	B1 2051–80	A2 2021–50	A2 2051–80	B1 2051–80	A2 2021–50	A2 2051–80	B1 2051–80
Mire species									
<i>Lagopus lagopus</i>	–20.7	–40.1	–23.7	8	68	28	–0.12	–0.35	–0.21
<i>Limnocyrtus minimus</i>	–66.1	–97.7	–94.8	74	194	178	–0.21	–0.29	–0.27
<i>Limosa lapponica</i>	–84.2	–99.6	–98.3	91	250	222	–0.39	–0.43	–0.43
<i>Numenius phaeopus</i>	–35.0	–70.5	–56.5	38	133	92	–0.27	–0.49	–0.40
<i>Tringa erythropus</i>	–73.0	–99.1	–97.5	89	276	180	–0.40	–0.58	–0.53
<i>Tringa nebularia</i>	–37.4	–67.9	–43.2	30	60	27	–0.24	–0.39	–0.25
<i>Limicola falcinellus</i>	–41.7	–87.8	–75.0	34	171	98	–0.09	–0.24	–0.19
<i>Phalaropus lobatus</i>	–42.8	–80.7	–61.0	28	85	55	–0.26	–0.37	–0.31
<i>Anthus cervinus</i>	–69.7	–95.5	–89.7	43	116	78	–0.32	–0.41	–0.38
<i>Emberiza pusilla</i>	–54.0	–97.5	–78.8	17	131	29	–0.19	–0.28	–0.24
<i>Calcarius lapponicus</i>	–85.0	–92.6	–92.5	66	91	74	–0.55	–0.61	–0.61
Mean (±S.E)	–55.4 ± 6.5	–84.4 ± 5.6	–73.7 ± 7.5	47 ± 9	143 ± 22	96 ± 20	–0.27 ± 0.04	–0.40 ± 0.04	–0.35 ± 0.04
Forest species									
<i>Buteo lagopus</i>	–56.8	–95.9	–85.3	47	152	107	–0.33	–0.66	–0.57
<i>Strix nebulosa</i>	–46.8	–83.6	–79.4	155	285	262	–0.19	–0.24	–0.23
<i>Surnia ulula</i>	–69.0	–94.1	–92.9	110	225	200	–0.25	–0.35	–0.34
<i>Perisoreus infaustus</i>	–15.5	–49.4	–29.6	18	88	50	–0.18	–0.41	–0.29
<i>Bombicilla garrulus</i>	–71.5	–97.8	–78.5	29	219	34	–0.30	–0.41	–0.33
<i>Parus cinctus</i>	–37.8	–95.1	–76.9	22	165	77	–0.37	–0.65	–0.55
<i>Fringilla montifringilla</i>	–32.1	–61.0	–48.7	48	145	94	–0.20	–0.43	–0.30
<i>Pinicola enucleator</i>	–83.2	–100.0	–98.8	57	–	251	–0.47	–0.54	–0.53
<i>Loxia leucoptera</i>	–98.6	–100.0	–100.0	246	–	–	–0.16	–0.18	–0.18
<i>Emberiza rustica</i>	–30.3	–37.3	–24.6	31	96	33	–0.19	–0.33	–0.19
Mean (±S.E)	–54.2 ± 8.3	–81.4 ± 7.4	–71.5 ± 8.7	76 ± 23	172 ± 24	123 ± 30	–0.27 ± 0.03	–0.42 ± 0.05	–0.35 ± 0.05
Species of mountain heaths									
<i>Lagopus muta</i>	–70.9	–97.6	–89.5	51	117	78	–0.30	–0.38	–0.36
<i>Charadrius morinellus</i>	–86.2	–98.9	–96.8	80	211	114	–0.24	–0.28	–0.27
<i>Calidris temminckii</i>	–51.4	–82.0	–68.2	20	55	37	–0.26	–0.37	–0.33
<i>Stercorarius longicaudus</i>	–85.3	–99.3	–97.5	53	209	177	–0.63	–0.71	–0.71
<i>Eremophila alpestris</i>	–58.0	–77.1	–60.3	59	78	65	0.03	0.02	0.06
<i>Plectrophenax nivalis</i>	–51.9	–58.8	–50.8	33	45	34	–0.14	–0.16	–0.11
Mean (±S.E)	–67.3 ± 6.5	–85.6 ± 6.6	–77.2 ± 8.2	49 ± 9	119 ± 30	84 ± 22	–0.26 ± 0.09	–0.31 ± 0.10	–0.29 ± 0.11
Total mean (±S.E)	–57.6 ± 4.3	–83.6 ± 3.7	–73.6 ± 4.6	58 ± 10	147 ± 14	103 ± 14	–0.27 ± 0.03	–0.39 ± 0.03	–0.33 ± 0.03

Change in distance to the nearest climatically suitable cell is the distance of projected occurrence cells in the future periods to the nearest occupied cell in the predicted distribution of 1971–1990 minus the predicted nearest occupied cell in 1971–1990. Both in change in distribution and in distance, threshold values based on prevalence were used when presence–absence cut-offs of species were interpreted (see text). In the change of probability of already occupied cells (no cut-off, original data), probability based on prediction in 1971–1990 was compared to that in later periods.

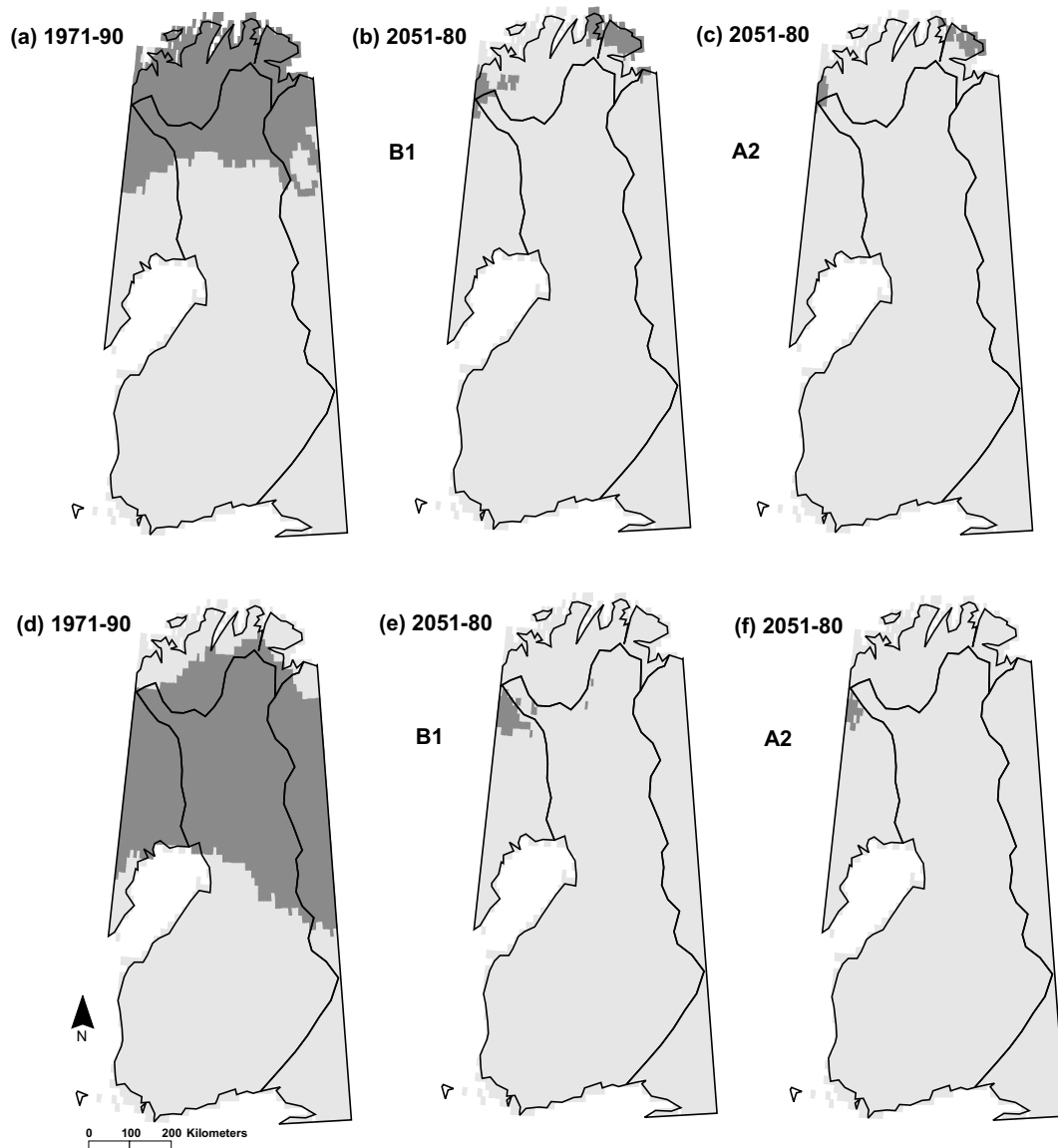


Fig. 3 – Predicted distribution with prevalence (%) of original data as a cut-off value for presence–absence for the red-throated pipit (*Anthus cervinus*) in 1971–1990 (a) and in 2051–2080 based on scenario A2 (b) and B1 (c), and that for the spotted redshank (*Tringa erythropus*) in 1971–1990 (d) and in 2051–2080 based on scenario A2 (e) and B1 (f).

2051–2080 (Table 2, Fig. 3). Based on scenario A2 the predicted area decrease by 2051–2080 was over 95% for 13 species and over 60% for 23 species. The climatically suitable area of the two-barred crossbill (*Loxia leucoptera*) was predicted to disappear both in scenarios A2 and B1, and that of the pine grosbeak (*Pinicola enucleator*) in scenario A2. In scenario A2 in 2051–2080 there were 14 species for which the number of predicted occupied cells was less than 100 (<2.5% of all squares).

In order to examine the possible bias of more inaccurately modeled species being projected to face more drastic range contractions than the more accurately modeled species, we related the explanatory power of the bioclimatic models to the predicted range loss for each species. However, there was no correlation between the explanatory power of the original model (deviance explained) and predicted percentage decline in the climatically suitable area based on scenario

A2 in 2051–2080 ($r = -0.089$, $p = 0.658$, $n = 27$). Moreover, there were no differences (A2 in 2051–2080) between species of different habitat types in the predicted area decrease (mire species, mean: -84.4% ; forest species: -81.4% , species of mountain heaths: -85.6% ; Kruskal–Wallis analysis of variance, $H = 0.037$, $p = 0.982$, $df = 2$). However, predicted range size (number of cells occupied) in 1971–1990 explained over half of the predicted distribution in 2051–2080 (scenario A2, $r^2 = 0.537$, $F_{1,25} = 29.01$, $p < 0.001$).

Change in distance from the nearest climatically suitable cell was on average 103 km in the B1 scenario and 147 km in the A2 scenario in 2051–2080 (Table 2). The greatest changes (>250 km) in the distances from the nearest climatically suitable cell in 2051–2080 (apart from species predicted to disappear) were for the great grey owl (*Strix nebulosa*) both in scenario A2 and B1. The climatic suitability of occupied grid

cells (predicted probability of occupied cells in 1971–1990) declined notably from 1971–1990 to 2051–2080, on average by 0.33 in scenario B2 and by 0.39 in scenario A1. The greatest change occurred in the long-tailed skua (*Stercorarius longicaudus*) in all the scenarios.

4. Discussion

4.1. Bioclimate envelope models in forecasting range declines

A comparison with other studies that have provided estimates of the projected loss of suitable climate for species (e.g. Iverson and Prasad, 1998; Crumpacker et al., 2001; Beaumont and Hughes, 2002; Erasmus et al., 2002; Peterson et al., 2004; Simmons et al., 2004; Thuiller et al., 2005; Ohlemüller et al., 2006a; Svenning and Skov, 2006) reveals that the projected mean loss of our study species is among the most severe projected species range contraction trends hitherto reported. This gives support to the hypothesis that the harmful impacts of climate change will be strongest at high latitudes. Similarly strong projected losses of species ranges have been revealed only in another region barred by sea areas, South Africa, where 18% of the study species were projected to totally lose their climatically suitable space, and 42% of the species to lose 27–99% of their current range (Midgley et al., 2003; see also Erasmus et al., 2002). As regards Europe, Thuiller et al. (2005) estimated that 22% of the studied species would face over 80% range loss (our “worst case scenario” was 48% of species losing >95% range loss), and Araújo et al. (2004) pointed out that species projected to lose their climatic envelope occurred mainly in southern Europe and Fennoscandia, the latter concurring with our findings.

It could be possible that predictive models with the greatest changes might be based originally on GAM models with low explanatory power. This artefact may have affected certain species, such as the disappearance of the two-barred crossbill, because the model of this species explained only 16.6% of the original geographic variation in species distribution in 1971–1990. However, there was no relationship between the deviance explained and the predicted change in climatic space in all species, indicating that there were no systematic biases that could be dependent on the explanatory power (% of deviance explained). Furthermore the model performance (AUC) was good or excellent for all but two species, for which it was fair (hawk owl *Surnia ulula*, two-barred crossbill).

Topography also affects patterns of predicted climate space of species. Peterson (2003) compared projected climate change effects on Rocky Mountain and Great Plains birds in western North America by 2050. He concluded that particularly flatland birds would lose a large proportion of their present distribution. Therefore landscape structure clearly affects the predicted range shifts of species, the area effects being much higher in a flatter landscape (Peterson, 2003). Most of the northern-boreal and continental arctic regions are rather flat, peneplain or gently sloping mountains, and thus species are more susceptible to climate change than in regions characterized by a rugged heterogeneous topography with varying climate.

4.2. Interactions with land cover and habitat changes

An important issue is how land cover and habitats preferred by the species are affected by the predicted climate change. We did not include land cover predictors in our models. Climate has been found to be the main driver of both species and land cover distributions in coarse scale studies in Europe (Pearson and Dawson, 2003; Thuiller et al., 2004), but at a finer scale (e.g. 10-km and 20-km resolutions) the integration of land cover may significantly contribute to the model accuracy of bird distributions (Luoto et al., 2007). Because of this our bioclimatic models partly provided overly optimistic projections of the species distributions: in particular, mountain heath or open mire species were predicted to occur in certain areas in which there was no suitable habitat available for them. Despite these limitations, the majority of the distributions of land bird species in Finland have been found to be correlated with climate (Luoto et al., 2007). Thus bioclimatic envelope models provide useful approximations of the climatically suitable regions for them, both currently and under projected future climates.

Only eight of the studied species (rock ptarmigan, Eurasian dotterel *Charadrius morinellus*, whimbrel *Numenius phaeopus*, red-necked phalarope *Phalaropus lobatus*, long-tailed skua, horned lark, Lapland longspur *Calcarius lapponicus*, snow bunting *Plectrophenax nivalis*) breed permanently in at least one of the islands or island groups of the Arctic Ocean (Iceland, Svalbard & Jan Mayen, Frans Josef Island, Novaja Zemlja, Greenland) north of continental Europe (Hagemeyer and Blair, 1997; BirdLife International, 2004), and five of these are species of mountain heaths in Fennoscandia. This means that 70% of the species in this study are totally dependent on the ecological conditions currently prevailing in continental Europe. These species are particularly vulnerable to climate warming, with high global extinction threats. Thus, large-scale geographical barriers coupled with climate-driven northward range shifts will clearly constitute a double jeopardy for northern species.

The negative impacts of the projected range contraction of northern birds are likely amplified in the future due to the forecasted changes in the amount and distributions of the preferred habitats, which are in line with the range shifts projected in this study (although the habitats themselves will obviously change at a slower rate). The studied species breed in coniferous or deciduous forests, in open mires or in mountain heaths. All these habitat types are expected to change considerably in the future. For example, due to upwards advancing treelines in Scandian mountains, treeless heaths are predicted to decline by 75–85%, with most of the remaining areas being scree slopes and boulder fields (Moen et al., 2004). Moreover, due to the future fragmentation of mountain heaths, the population sizes of bird species will most probably be even smaller than the direct habitat decrease suggests. In our modeling the range size of species of mountain heaths was forecasted to decline by 86% based on scenario A2.

Considerable changes are also expected to occur in boreal forests by 2100, including the predicted decrease of coniferous tree stands, particularly Norway spruce in Fennoscandian boreal forests, where birches (*Betula pendula* and *B. pubescens*) will probably replace coniferous trees (Kellomäki et al., 2001, 2005; Koca et al., 2006). Because several species in our study,

such as Siberian jay (*Perisoreus infaustus*), Siberian tit (*Parus cinctus*), and pine grosbeak prefer old-growth coniferous forests (Virkkala, 1991a; Virkkala and Rajasärkkä, 2007), the predicted decrease of coniferous stands will be detrimental to these species. The populations of these species will also be further reduced and threatened by fragmentation of old-growth forests in Fennoscandia due to large-scale logging (Virkkala, 1991a). In contrast to situation in fragmented landscapes, these species had not decreased in large, uniform old-growth forest areas (Virkkala, 1991b), which implies the importance of protecting large areas of native habitats in a rapidly changing climate.

The potential climate change – habitat change interactive threats for birds inhabiting coniferous forests were also observed in a study by Ohlemüller et al., 2006a focusing on European woody species: the authors showed that among the studied 17 tree species the boreal and temperate species lose most of their suitable climate in Europe between 1945 and 2095 based on two different climate scenarios. In particular, Norway spruce was predicted to lose over two thirds but also Scots pine between about one half and three quarters of their range in the scenarios (Ohlemüller et al., 2006a).

5. Concluding remarks

Tundra species may survive in the Arctic Islands, but northern-boreal forest and mire species occurring in continental areas may become more easily regionally or globally extinct in the long run. In our study we showed that boreal forest and mire bird species were projected to lose as much of their range as those of the tundra (mountain heath) species. Therefore particular attention should be paid to northern-boreal forest and mire species when preserving global biodiversity in the changing climate of the 21st century. To reduce the negative effects of climate change on the northern species particularly coupled with detrimental land use, relatively large areas of continuous habitats in a connected network of protected areas should be preserved (see Virkkala, 1991b; Virkkala and Rajasärkkä, 2007).

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