RESEARCH ARTICLE

Preserving species populations in the boreal zone in a changing climate: contrasting trends of bird species groups in a protected area network

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Abstract

A protected area network should ensure the maintenance of biodiversity. Because of climate change, species ranges are expected to move polewards, causing further demand for the protected area network to be efficient in preserving biota. We compared population changes of different bird species groups according to their habitat preferences in boreal protected areas in Finland on the basis of large-scale censuses carried out in 1981–1999 and in 2000–2009. Population densities of common forest habitat generalists remained the same between the two periods, while densities of species of conservation concern showed contrasting trends: species preferring old-growth forests increased, but those living on mires and wetlands, and species of Arctic mountains decreased. These trends are most probably connected with climate change, but successional changes in protected areas and regional habitat alteration should also be taken into account. Of species preferring old-growth forests, a larger proportion are southern than among species of mires and wetlands, or of Arctic mountains, most or all of which, respectively, had a northerly distribution. In general, northern species have decreased and southern increased with the exception of northern species of old-growth forests which had not declined. On the other hand, bird species of mires and wetlands decreased also in the northernmost protected areas although mires had not been drained in the region in contrast with southern and central Finland thus indicating that regional-scale direct habitat loss did not cause the decline of these species in the north. It is suggested that climate change effects on species in natural boreal and Arctic habitats most probably are habitat-specific with large differences in response times and susceptibility.

Introduction

A protected area network should ensure the maintenance of species and communities. However, a reserve network is rarely adequate for this purpose (Gaston et al. 2008, Rodrigues et al. 2004). Furthermore, the climate is changing rapidly and, consequently, species ranges are expected to move polewards (Parmesan 2006, Hitch and Leberg 2007, Huntley et al. 2007, Huntley et al. 2008, Zuckerberg et al. 2009) creating further demand for the protected area network to be efficient in preserving biota (Araújo et al. 2004, Hannah and Salm 2005, Hannah et al. 2007). Because of climate change, species distributions shift and networks of reserves may cease to afford protection to those species for which they were originally established (Coetzee et al. 2009, Hole et al. 2009, Araújo et al. 2011). Species and communities in northern boreal and Arctic regions face particular risk from climate change because the Arctic Ocean represents an effective natural barrier to northward range shifts of northern boreal terrestrial species (Virkkala et al. 2008, 2010). Loarie et al. (2009) compared the world's 14 main biomes and protected areas situated within them and showed that climate residence time by 2100 was among the lowest in protected areas situated in boreal forests. This would mean that the climate in protected areas of boreal forests could see the greatest amount of change on a global scale.

Climate-change-driven range shifts are probably among the most dramatic at northern latitudes because of the greater temperature increase projected for these regions (Jetz et al. 2007). For example, in Finland, according to the worst-case climate change scenario, mean annual temperature will increase by as much as 7 °C by 2080 in comparison with the baseline period, 1961–1990 (Jylhä et al. 2004). Annual mean temperatures in Finland increased by 0.7 °C in 1901–2000 with most of the increase at the end of the century (see Jylhä et al. 2004).

An important issue for future conservation planning is what the functionality of the present protected area network is in the face of climate change (Hole et al. 2011). The protected area network should enhance species to survive in a changing climate. Many species are already threatened by intensive human land use that is causing habitat loss.

In northern Europe, the boreal landscape has been intensively utilized; in particular, forestry, alongside agriculture, is the major use of land in vast areas. Natural, old-growth forests have been logged and mires drained for forestry and agricultural purposes. In Finland (Fig. 1) both mires and old-growth forests, in particular, have been regarded as focal habitats for species and communities in terms of conservation, and specific protection programs for both of these habitats have been launched and implemented (OECD 1997, Auvinen et al. 2010). About 12% of all mires and 25% of undrained ones are protected, with a total land area of about 11,000 km^2 (Virkkala et al. 2000). Over 5% (10,700 km^2) of forest land and about half of remaining
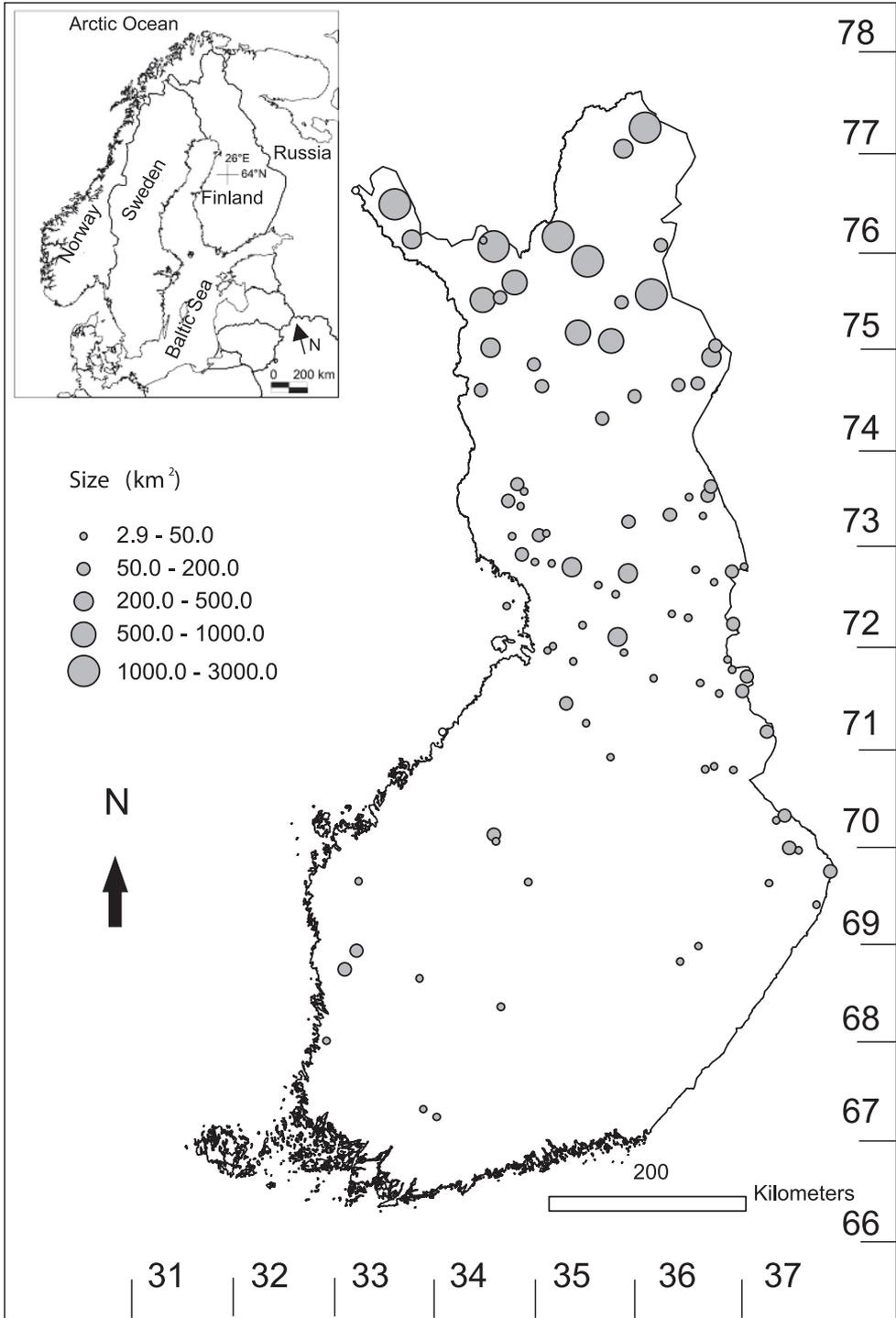
Figure 1. Location of the protected areas in Finland, where bird censuses were carried out both in 1981–1999 and in 2000–2009. Uniform grids (Uniform Coordinate System) used in Finland are presented.

old-growth forests are protected. In spite of the protection programs and many other protected areas (e.g., national parks, wilderness areas, and strict nature reserves) the proportion of protected areas is fairly low in the southern part of Finland, where land use intensity is the highest. In contrast, the protected area network is much larger and more representative in the northern part of Finland (Virkkala et al. 2000, Virkkala and Rajasärkkä 2007). About 80% of the protected land is in northern Finland, in the northern boreal zone (Virkkala et al. 2000).

Direct habitat loss outside protected areas may influence populations of species of conservation concern in protected areas, such as birds breeding on mires and wetlands in southern and central Finland, where over 70% of mires have been drained (Virkkala et al. 2000). In contrast, in the northernmost Finland mires have not been drained (Virkkala et al. 2000), and therefore population changes in protected areas there may not be caused by regional-scale habitat loss. Protected areas are also clearly the largest in the northernmost Finland further reducing the impact of regional human-caused habitat alteration on species populations (see Virkkala 1991). However, we have clear gaps in our knowledge dealing with the effect of the intensity of regional habitat alteration on biodiversity in boreal protected areas.

In this work, we compare in Finnish protected areas population changes of different bird species groups, which are classified according to species habitat preferences. We compare densities by referring to large-scale bird censuses performed in 1981–1999 and in 2000–2009. We have previously shown that northern bird species had declined and southern species increased between the two time slices (Virkkala and Rajasärkkä 2011a, 2011b). In this paper we extend our study of bird population changes in protected areas in relation to species habitat preferences with special emphasis on species of conservation concern. Direct human-caused habitat changes in protected areas have been minor between these time slices because human land use, such as logging and drainage of mires, is not allowed in these areas. In addition to habitat preference, we take into account distribution patterns of species. Here we address the following questions: How successful and efficient has the foundation of boreal protected areas been in terms of maintenance of species populations? Does the protected area network manage to preserve the species of conservation interest – i.e., particularly species preferring old-growth forests and species of mires and wetlands – in a changing climate?

Because land use intensity outside protected areas is different in the different parts of the country, we compare population changes of bird species groups also by taking the location of protected areas into account in order to separate the possible effects of regional habitat alteration (direct habitat loss and degradation outside protected areas) and climate change effects. If regional habitat alteration was the primary cause for population changes, the negative population changes should be more pronounced in the southern than in the northern protected areas both due to more intensive land use outside protected areas and smaller size of reserves in southern Finland. On the other hand, as a consequence of warming climate southern species are predicted to increase and northern species to decline (Jiguet et al. 2010, Kujala et al. 2011).

Material and methods

Protected areas

The total area of reserves (N = 96) in Finland (60–70°N, 21–31°E, Fig. 1) in which bird counts were done was 22,493 km^2, with the protected areas studied ranging in size from three to 2,524 km^2 (mean = 234.3 km^2, median = 51.6 km^2). Logging or drainage of mires is prohibited in the protected areas, so forestry is not allowed in these areas. Reindeer herding is a common use in northern Finnish protected areas. The protected areas studied accounted for over 60% of the land area of Finnish protected areas. Six areas were smaller than 10 km^2 and six larger than 1,000 km^2. The latter largest areas included four wilderness areas and two national parks in northernmost Finland. Twenty-four protected areas were studied in the southern half of Finland (total size: 910 km^2) and 72 in the northern half (total size: 21,583 km^2, see Fig. 1). Most of the protected land is in northern Finland (Virkkala et al. 2000, Virkkala and Rajasärkkä 2007). Forests cover 56% of the land in the reserves studied, with the rest being open mires and mountain areas. In southern half of Finland forests covered 70.0% and in northern half 55.4% of the land in the protected areas. Over two thirds of the protected forest stands are over 100 years old (Virkkala et al. 2000).

Bird censuses

Land birds in protected areas were counted by means of the Finnish line transect census method (Järvinen and Väisänen 1976), which is suitable for counting birds over large areas (Väisänen et al. 1998, Virkkala and Rajasärkkä 2007). The line transect method applies a one-visit census in which birds are counted during breeding season along a transect with an average length of 5–6 km.

The census is carried out in June in the early morning, when the singing activity of birds is highest. In the line transect method, a 50-meter-wide main belt along the walking line (25 m on each side) and a supplementary belt outside the main belt are separated. The latter covers all birds observed outside the main belt (e.g., Järvinen and Väisänen 1976, Järvinen et al. 1991, Väisänen et al. 1998, Virkkala 2004). In the Finnish line transect, densities of species based on the observations in the censuses are calculated in standard units of pairs/km^2. A pair was inferred from a male heard singing, from an otherwise observed male or female or from a group of fledglings according to the instructions of the Finnish line transect census (for details, see Järvinen and Väisänen 1976, Järvinen et al. 1991).

Densities of bird species (pairs/km^2) were calculated on the basis of observations in the whole survey belt, including both main and supplementary belts. Species-specific correction coefficients were used in the density calculation. These coefficients vary according to the proportion of main belt observations to all survey belt observations.

The density of a species (D, pairs/km^2) based on the Finnish line transect census was calculated as:

D = K × N/L, (1)

where K = species-specific correction coefficient, N = number of observations of a species on the whole survey belt, and L = transect length (in km). The species-specific correction coefficient (K) was calculated as (Järvinen and Väisänen 1983):

K = 40 – 40 √ (1– p), (2)

where p = proportion of main belt observations (range 0–1); for details of the calculations, see Järvinen and Väisänen (1983).

The species-specific correction coefficient takes into account the differing audibility and other detectability of different species (Järvinen and Väisänen 1983). The value of this coefficient is low for a species for which only a small proportion of all observations come from the main belt (e.g., the cuckoo *Cuculus canorus*). By contrast, the coefficient's value is high for species for which a large proportion of the observations are made in the main belt (e.g., the capercaillie *Tetrao urogallus*). In addition, detectability of a species may change during the breeding season, such as in the case of the black grouse *Tetrao tetrix*, of which the lekking period with singing (lekking) males usually ends by mid-June (see Appendix). All correction coefficients used in this study were calculated on the basis of line transect data collected from protected areas in Finland and neighboring countries in the boreal and hemiboreal vegetation zones. Species-specific correction coefficients used are presented in the Appendix.

The total length of line transect censuses in the protected areas was 6,587 km in 1981–1999 and 5,087 km in 2000–2009. Birds were counted in 96 areas, in which in both periods the total length of transects was at least 10 km (see Fig. 1). The median total length of transect kms in a protected area was 45.0 km in 1981–99 and 33.6 km in 2000–2009. The mean number of years that censuses were carried out in each protected area was 3.7 (median = 3) in 1981–99 and 2.4 (median = 2) in 2000–2009. The median census year was 1992 in the first and 2006 in the second period, making the average time span in the study 14 years. The same transects were not repeated, but censuses in each protected area included the same proportion of habitats in the two periods. Transects covered all main habitats in each studied protected area relative to each habitat's proportion.

Analyses

Bird species were divided into classes according to habitat preferences, in line with the classification applied by Virkkala et al. (1994) and Väisänen et al. (1998). In these classifications different groups of species of mires and wetlands were combined in the present study, as too were different groups of species of deciduous forests and species of bushes. Species of Arctic Lapland grouped together by Väisänen et al. (1998) were divided into species of Arctic mountain heaths and species of mires and wetlands.

The study used, all told, seven groups of species categorized by habitat preferences (see Appendix): (1) forest habitat generalists, (2) species of coniferous forests, (3) species preferring old-growth or mature forests, (4) species preferring deciduous forests

and bushes, (5) species of mires and wetlands, (6) species of cultivated areas, and (7) species of Arctic mountain heaths. Many species of cultivated areas also breed in natural habitats such as the fieldfare *Turdus pilaris* and hooded crow *Corvus corone cornix* in forests or the curlew *Numenius arquata* on mires. In total 148 species were included in the analyses. All land birds observed along the transects were included in these habitat preference groups except the swallow *Hirundo rustica* and the house martin *Delichon urbica*, which breed on buildings and were excluded.

Bird species were categorized also according to their distribution (see Appendix). Distribution pattern (southern or northern) was classified in terms of distribution and regional density variation in Finland (Väisänen et al. 1998). Species without any northward or southward pattern in their regional density or species with wide-ranging sporadic distribution were regarded as a separate class ('whole country').

Densities of species between the two time periods were compared pairwise in each protected area via either paired *t*-test or non-parametric Wilcoxon signed rank test. A non-parametric test was adopted when the prerequisites for use of a parametric test were not fulfilled. For these analyses species densities were summed in each of the habitat preference class before pairwise comparison. Because the statistical tests were not independent between the comparisons, significant differences were based on sequential Bonferroni correction (Rice 1989).

Next, in a combined analysis, habitat preference class and distribution pattern were compared through repeated measures analysis of variance (ANOVA). Time (periods) represents here a quantitative, repeated factor, the effects of which can be examined via within-subject contrasts (e.g., Gurevitch and Chester 1986; Quinn and Keough 2002). Habitat preference class and distribution pattern were regarded as between-subjects factors in the analysis. We took into account in the analysis all species observed in at least two thirds of the protected areas in both periods (in 64 out of 96 areas, 37 species). This was essential because parametric statistical analyses were adopted and the other, less common species were non-normally distributed in protected areas as a result of the high proportion of zero classes. Bird pairs in these 37 common species studied constituted the vast majority of the bird communities, 88% of all bird pairs in protected areas.

Change in the average density of each habitat preference group was compared in each of the protected area between the two time slices (n = 96). Percentage changes in density in each of the protected areas were used. Percentage changes above and below 100% are not strictly comparable; for example, a doubling increase from 100 gives a value of 200, but a similar decrease to half that yields 50. To avoid this discrepancy, we used logarithmic ratio (log ratio) of per cent change in densities, where, for example, 100% increase in density from 1981–1999 to 2000–2009 would be log (200/100) = +0.301 and 50% decrease is log (50/100) = –0.301. In a linear regression analysis we used location (south-north) and size of a protected area (log-transformed) as predictive (explanatory) variables for the temporal density changes of the different bird groups. South-north location and size of protected area are positively correlated (r = 0.629, p<0.001) i.e. largest protected areas are situated in the northernmost Finland.

Densities of bird species between the two time periods were compared also based on IUCN threat categories in Finland (Rassi et al. 2010), which included threatened and near threatened species and species of least concern (see Appendix). Critical, endangered and vulnerable classes were regarded as threatened.

Results

The mean temperature of the coldest month (February) and that of April–June essential for bird species (see Heikkinen et al. 2006, Virkkala et al. 2008) were compared from Finnish Meteorological Institute data. The mean temperature of the coldest month rose by 0.8 °C (1981–1999: –9.46 °C, 2000–2009: –8.66 °C) and that for April–June by 0.7 °C in Finland (1981–1999: 6.71 °C, 2000–2009: 7.43).

Population changes of species groups based on habitat preferences in 1981–1999 and in 2000–2009 are presented in Table 1. The mean density of forest habitat generalists did not change from 1981–1999 to 2000–2009. Forest habitat generalists accounted for more than half of all breeding bird pairs (55–56%) in protected areas. Densities of species of coniferous forests and species preferring old-growth and mature forests increased, while species of deciduous forests and bushes, species of mires and wetlands, and species of Arctic mountains decreased between the two time slices (see Table 1). In proportional terms, the largest decrease was in species of Arctic mountains, which declined to less than half (–57%), and the largest increase in species preferring old-growth and mature forests, which increased by 29%.

Densities of southern species increased significantly in forests habitat generalists, in species of coniferous forests and in species preferring old-growth or mature forests from 1981–1999 to 2000–2009 (Table 2). Densities of northern species decreased significantly in forest habitat generalists, in species of coniferous forests and in species of mires and wetlands. Species of coniferous forests distributed across the whole country increased (Table 2).

Table 1. Mean densities (pairs/km^2 ± standard error) of bird species groups with different habitat preferences in 1981–1999 and in 2000–2009. Statistical test (N = 96) by paired t-test or Wilcoxon signed rank test (species of Arctic mountains). Number of species in each species group in parentheses.

Species group	1981–1999	2000–2009	t	z	p[a]	Ranks[b]
Forest habitat generalists (15)	63.15±3.66	60.38±3.02	1.170	–	0.245	–
Species of coniferous forests (26)	17.75±1.42	20.65±1.49	4.079	–	**<0.001**	–
Species preferring old-growth or mature forests (14)	2.83±0.21	3.64±0.27	3.848	–	**<0.001**	–
Species preferring deciduous forests and bushes (23)	3.27±0.67	2.49±0.52	2.633	–	**0.010**	–
Species of mires and wetlands (36)	22.41±2.47	18.65±2.04	3.210	–	**0.002**	–
Species of cultivated areas (23)	2.27±0.24	2.88±0.34	2.083	–	0.040	–
Species of Arctic mountains (11)	0.37±0.15	0.16±0.07	–	2.561	**0.010**	7/23/66

[a] Significant differences (bold) are based on sequential Bonferroni correction.
[b] Ranks between 2000–2009 and 1981–1999: positive/negative/tied.

Table 2. Densities of species groups with different habitat preferences (p/km² ± s. e.) according to distribution pattern. Statistical significance is based on paired t-test (df = 95) or Wilcoxon signed rank test (N=96). Number of species in each group in parentheses. All Arctic mountain species are northern (see Table 1) and no species of cultivated areas is northern.

Distribution pattern	1981–1999	2000–2009	t	z	p[a]	Ranks[b]
Forest habitat generalists						
Southern species (5)	13.76±1.96	18.19±2.11	4.686	–	**<0.001**	–
Northern species (2)	12.93±0.93	10.06±0.82	3.924	–	**<0.001**	–
Whole country[c] (8)	36.46±2.12	32.13±1.59	2.611	–	0.010	–
Species of coniferous forests						
Southern species (16)	11.61±1.23	14.34±1.36	4.915	–	**<0.001**	–
Northern species (6)	2.41±0.22	1.63±0.18	4.569	–	**<0.001**	–
Whole country (4)	3.74±0.24	4.68±0.29	4.068	–	**<0.001**	–
Species preferring old-growth or mature forests						
Southern species (6)	1.08±0.14	1.68±0.19	5.385	–	**<0.001**	–
Northern species (6)	0.99±0.12	1.08±0.12	0.770	–	0.443	–
Whole country (2)	0.76±0.07	0.88±0.08	1.182	–	0.240	–
Species preferring deciduous forests and bushes						
Southern species (20)	2.70±0.66	2.06±0.52	2.386	–	0.019	–
Northern species (2)	0.56±0.20	0.42±0.13	–	1.304	0.192	21/15/60
Whole country (1)	0.01±0.00	0.01±0.01	–	0.350	0.727	6/7/83
Species of mires and wetlands						
Southern species (8)	0.02±0.01	0.02±0.01	–	0.751	0.452	14/16/66
Northern species (22)	19.08±2.26	15.63±1.86	3.248	–	**0.002**	–
Whole country (6)	3.30±0.62	2.99±0.60	1.184	–	0.239	–
Species of cultivated areas						
Southern species (15)	0.52±0.09	0.65±0.12	1.658	–	0.101	–
Whole country (8)	1.75±0.19	2.23±0.26	1.971	–	0.052	–

[a] Significant differences in bold (sequential Bonferroni correction for all the comparisons).
[b] Ranks between 2000–2009 and 1981–1999: positive/negative/tied.
[c] Whole country = species distributed throughout the country.

In the repeated measures ANOVA carried out for the most common 37 species, there was a significant difference both in the habitat preference and in the distribution pattern (Table 3). However, the statistical significance for the distribution pattern ($F = 38.16$, $p < 0.001$) was much more pronounced than for the habitat preference ($F = 3.06$, $p = 0.016$; Table 3). Northern species decreased and southern species increased in the different habitat preference classes (Fig. 2). Interaction between factor levels and the two between-subject factors (habitat preference and distribution pattern) was significant ($F = 9.631$, $p < 0.001$), which was mainly due to the fact that species distributed across whole country included both increased and decreased species (see Fig. 2).

The regression model with south-north location and size of protected area as predictive variables explained significantly only population changes of species of coniferous forests, and this species group increased most in the northern Finnish protected areas (Table 4, Fig. 3A). In other species groups location and size of protected area did not affect population changes observed (for species of mires and wetlands, see Fig. 3B).

Table 3. Results of within-subject contrasts of repeated measures analysis of variance (ANOVA). Factor levels (within-subject): density in 1981–1999 and 2000–2009; between-subjects factors: habitat preference (habitat), distribution pattern. * = Interaction between factor levels and different between-subjects factors.

Source	[a]df	[b]MS	F	p
Factor	1	27.331	6.030	0.014
Factor*species	1	5.548	1.224	0.269
Factor*protected areas	1	20.926	4.617	0.032
Factor*habitat	2	13.878	3.062	0.016
Factor*distribution	2	172.970	38.161	<0.001
Factor*habitat *distribution	3	43.654	9.631	<0.001
Error (factor)	3539	4.533		

[a]df = degrees of freedom.
[b]MS = mean squre.

Table 4. Regression analyses based on location (south-north coordinates) and size of a protected area (log-transformed) as predictors affecting the temporal density changes of species groups with different habitat preferences. $df_{regression}$ = 2, $df_{residual}$ = 93. The values (B) and significance (based on t-test) of the standardized coefficients are presented. Standardization of the coefficient shows which of the independent variables have a greater effect on the dependent variable, when the variables are originally measured in different units (see Quinn and Keough 1982).

Species group	[a]r²	[b]MS	F	p	Standardized coefficients					
					Location			Size		
					B	t	p	B	t	p
Forest habitat generalists	0.044	0.069	2.145	0.123	0.254	1.944	0.055	–0.087	0.668	0.506
Species of coniferous forests	0.154	0.499	8.480	<0.001	0.365	2.976	0.004	0.042	0.340	0.735
Species preferring old-growth or mature forests	0.017	0.145	0.800	0.452	–0.137	1.039	0.302	0.012	0.093	0.926
Species preferring deciduous forests and bushes	0.004	0.092	0.165	0.848	0.060	0.451	0.653	-0.075	0.560	0.577
Species of mires and wetlands	0.015	0.064	0.685	0.507	–0.117	0.882	0.380	–0.006	0.043	0.966
Species of cultivated areas	0.013	0.113	0.628	0.536	–0.110	0.831	0.408	–0.008	0.062	0.951

[a]r² = coefficient of determination
[b]MS = mean square

Densities of both threatened and near threatened bird species decreased significantly from 1981–1999 to 2000–2009, while density of the other species (least concern) did not change between the two time periods (Table 5).
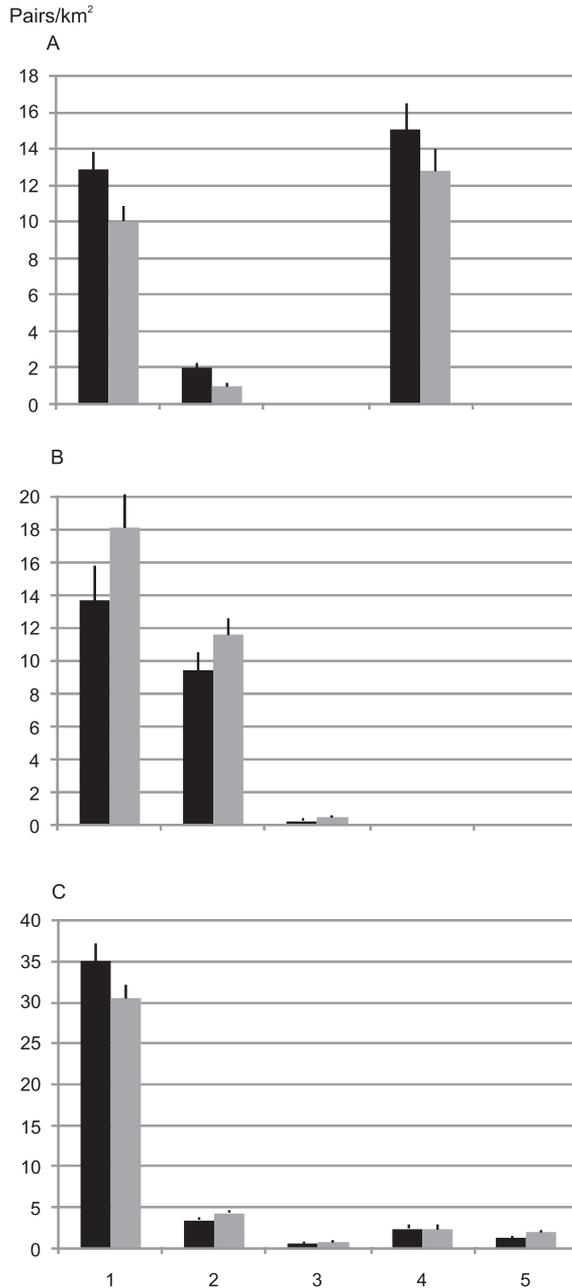
Pairs/km²

Figure 2. Mean density (pairs/km²±S.E.) of different bird species groups (most common species) in protected areas in 1981–1999 (black columns) and in 2000–2009 (gray columns). **1** = forest habitat generalists, **2** = species of coniferous forests, **3** = species preferring old-growth or mature forests, **4** = species of mires and wetlands, **5** = species of cultivated areas. **A** northern species **B** southern species **C** species distributed over the whole country. Northern species preferring old-growth forests, southern species of mires and wetlands, and both southern and northern species of cultivated areas were not included in the analysis due to their rarity or absence.
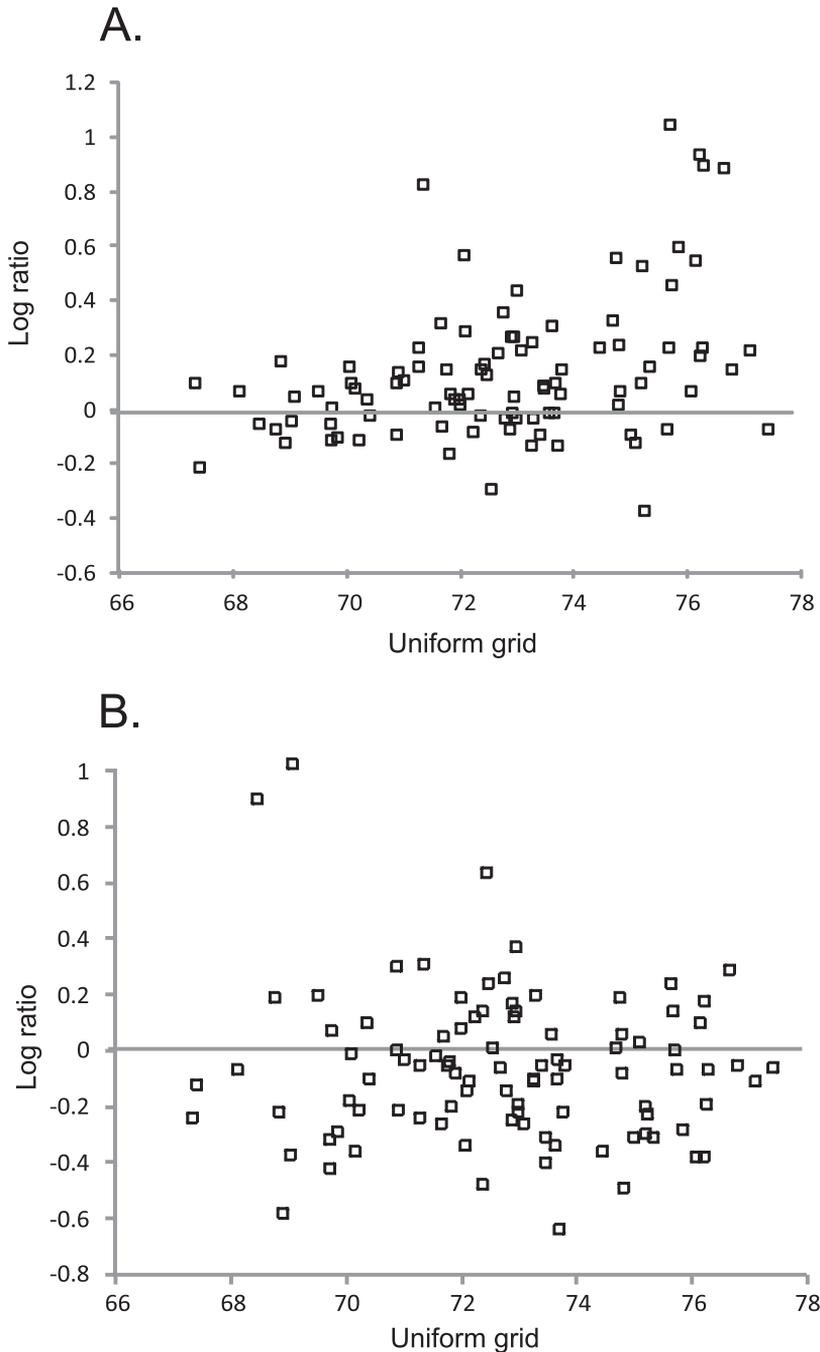
Figure 3. Change in the average density of species of coniferous forests (A.) and species of mires and wetlands (B.) from 1981–1999 to 2000–2009, based on log ratio [log ratio = log (density in 2000–2009/ density in 1981–1999)] in each protected area (n = 96) according to location from south to north (for uniform grid, see Figure 1). Values of log ratio above zero (line) show population increase and those below zero population decline in each protected area.

Table 5. Densities (pairs/km^2 ± s.e.) of bird species groups according to IUCN threat status (threatened, near-threatened, least concern, see Appendix) in Finland in 1981–1999 and in 2000–2009. Statistical test (df = 95) by paired t-test. Number of species in each species group in parentheses.

IUCN category	1981–1999	2000–2009	t	p
Threatened (23)	8.53±0.67	5.63±0.50	6.142	<0.001
Near threatened (19)	10.18±0.81	8.25±0.66	3.714	<0.001
Least concern (106)	93.35±5.16	94.97±4.64	0.510	0.611

Discussion

We observed that patterns in the population changes of the different bird species groups varied considerably. Moreover, there were large within-species-group differences in population trends when distribution pattern of species was taken into account. At a European scale Gregory et al. (2009) observed, based on bird censuses in 1980–2005, that species predicted to expand their ranges due to climate change have increased and species predicted to lose ranges have decreased. Our results of bird population changes in boreal protected areas are in line with the results of Gregory et al. (2009), but it is further suggested that climate change effects on species in natural boreal and Arctic habitats most probably are habitat-specific with large differences in response times and susceptibility.

The species of greatest conservation interest in terms of land-use pressures showed interesting patterns: species preferring old-growth or mature forests have contrasting trends with the species of mires and wetlands in the protected area network. Preserving old-growth forests seem to have clearly benefited species preferring these habitats in Finland, while species of mires and wetlands have decreased in spite of fairly large-scale protection of these habitats. However, an important point here is that a much larger proportion of bird pairs in species preferring old-growth forests are southern (38–46%) than the equivalent figure among species of mires and wetlands (0.1%). There was a general pattern in the different species groups that northern species had decreased and southern species had increased, which is in line with the predictions of range shifts of species both in Europe and in Fennoscandia (Huntley et al. 2007, Huntley et al. 2008, Virkkala et al. 2008, 2010, Kujala et al. 2011, Barbet-Massin et al. 2012).

Also species of Arctic mountains have decreased, although about 90% of mountain heaths are within protected areas (Virkkala et al. 2000). All species of Arctic mountains and 85% of bird pairs of mire and wetland species were northerly distributed. This further suggests that climate change has a considerable effect on population changes of these species groups. Species of Arctic mountains is also the species group with clearly the highest proportion of threatened species: over half (six species) of the 11 species is regarded as critical, endangered or vulnerable with additional three species being near threatened (see Appendix).

Moreover, species of mires and wetlands have decreased also in large protected areas situated in northernmost Finland (see Fig. 3B), in which region (north of the uniform grid 74 in Fig. 1) mires have not been ditched at all (Virkkala et al. 2000). Therefore, the decrease of species of mires and wetlands in the northern protected

areas cannot be explained to be caused by drainage of mires outside protected areas. Northern Finnish habitats both in protected and in unprotected areas are grazed by reindeers, which may have an effect also on bird species densities.

In a recent study, Kujala et al. (2011) further showed in the most common bird species that northerly-distributed species were well-represented in the Finnish protected area network, but the population trends of these species are currently declining in Finland most probably reflecting changes in climate. In addition, southerly-distributed species with poor coverage in protected areas are increasing.

Forest habitat generalists had not increased, in contrast with the other species group in which species have large habitat amplitudes – namely, species of coniferous forests. These species occur in variable coniferous woods without strict habitat preferences. As in the comparison of species groups of greatest conservation interest (species preferring old-growth forests vs. species of mires and wetlands), a much larger proportion of species and bird pairs of coniferous forests are southern (about 55%) than among forest habitat generalists (20–30%, see Table 2), which probably explains the different patterns of population changes in these species groups. The increase of species of coniferous forests was most pronounced in the northernmost protected areas (Fig. 3A). This probably reflects the fact that southern bird species have increased most at their northern range boundary occurring in northernmost Finland (Virkkala and Rajasärkkä 2011b). Populations of species preferring coniferous forests are probably also affected by the overall increase in coniferous wood volume due to, for example, drainage of mires and increased annual increment of the growing stock (wood volume), which is also affected by increased temperatures. Moreover, in a previous study, Virkkala and Rajasärkkä (2011a) showed that migratory patterns could not explain the population changes observed among bird species in Finnish protected areas.

The decrease of species of deciduous forests and bushes may be caused by the fact that many of these species occur in early succession forest habitats which have changed as a consequence of forest succession in many of the studied protected areas during the study period. Many bird species prefer early succession forest habitats and disappear or decline, when forest maturates (see Helle 1985, Helle and Mönkkönen 1985).

Forest succession probably also affects the increase of southern old-growth forest species, because in southern Finland many forests in protected areas have previously been managed and therefore forests are much younger there than in northern Finnish protected areas (Virkkala et al. 2000), where old-growth forests were prevailing already at the time of foundation of protected areas. In southern Finland, previously managed and younger forests in reserves have matured and developed probably as more suitable to the species preferring old-growth or mature forests during the average study period of 14 years. However, according to the comparison of the results of Finnish bird atlases in 1974–89 and in 2006–2010, many of the southern species of old-growth and mature forests have increased and enlarged their ranges in Finland, such as the red-breasted flycatcher *Ficedula parva* and treecreeper *Certhia familiaris* (see Valkama et al. 2011).

Bird species populations in protected areas have thus been affected by climate change, successional habitat changes in protected areas and probably also landscape-level habitat

changes outside protected areas. The latter two factors cannot however explain the general, overall increase of southern species and decrease of northern species (Tables 2 and 3 and Fig. 2). Moreover, two-thirds of the threatened species in our data (15/23) are northern.

There might be a relation between climate niche, habitat niche and range size affecting population trends of species. Barnaugaud et al. (2012) observed in studying climate and habitat niches of French birds that species with narrow thermal breadths were also more often habitat specialists. We did not study climate niches of bird species but in general southern species probably have larger ranges and also larger climate niches than northern species. So there may be a positive correlation between climate niche and population trend, but this issue should be properly studied.

Specialist species might be more susceptible to climate change than habitat generalists (Jiguet et al. 2007, Devictor et al. 2012). However, in our study specialist species of old-growth forests had not declined in contrast with specialists of wetlands and mires. In addition, forest habitat generalists consisted of both declined northern species and increased southern species. So there seems not to be any general pattern between habitat niche breadth and population trend of species in our data, but also this issue should be studied in more detail.

Densities of northern species have generally declined (Virkkala and Rajasärkkä 2011a). However, population densities of northern species preferring old-growth forests remained the same, so the patterns are not always unambiguous: different species and species groups are affected in a different manner by several factors, including climate change and land use. For northern species preferring old-growth forests, the large northern protected area network – over 40% of forests are protected in northernmost Finland (Virkkala et al. 2000, Virkkala and Rajasärkkä 2007) – may have mitigated the negative effects of climate warming. This might be because climate factors may affect old-growth forests more slowly than they do mires or Arctic mountain heaths. Thus, also the response time to changes in climate and land cover varies between species and between species groups. For some species conditions become more suitable through both climate-induced and land-use changes while other species are highly susceptible to changes in their habitat (see also Matthews et al. 2011).

In a recent work dealing with protected area networks in Canada, it was observed that butterfly populations had declined both in protected and in non-protected areas, suggesting that existing reserve networks have provided little buffer against the impacts of climate change on butterfly species richness (Kharouba and Kerr 2010). In Finnish protected areas, the same seems largely to hold true for northerly distributed birds, since these birds have mostly, with the exception of species preferring old-growth forests, declined regardless of their habitat preferences. On the other hand, southern species preferring old-growth forests have increased in Finnish protected areas. So the pattern maybe more complicated than that observed by Kharouba and Kerr (2010) in Canada. It seems that both distribution pattern and habitat preferences of species affect population changes of species in boreal protected areas, in addition to the quantity and quality of protected areas.

Mires and mountain heaths change more rapidly in consequence of climate warming than old-growth forests, for which reason populations on mires and mountain heaths are also more affected by climate change. For example, in northernmost Europe, wet, structurally diverse palsa mires created by permafrost are expected to decline and become more homogeneous fairly rapidly in the coming decades as a consequence of climate warming (Fronzek et al. 2010), resulting in decreased abundance of bird populations, such as many wader species found in these ecosystems (Luoto et al. 2004). Furthermore, species-rich boreal aapa fens are changing into drier bogs because of climate warming (Tahvanainen 2011). As a result of upward-advancing treelines in Scandian mountains, treeless heaths are predicted to decline by 75–85%, with most of the remaining areas being slopes and boulder fields (Moen et al. 2004). As a consequence of climate change, vegetation changes in Arctic mountains are predicted to be considerable and rather rapid (Sormunen et al. 2011). On the other hand, stand age of natural old-growth forests in Fennoscandia is typically over 200 years or even 300 years with stand cohorts of over 150 years dominating (Kuuluvainen 2002, Pennanen 2002). Therefore, climate probably also affects bird communities in mires and on mountain heaths more rapidly than those in old-growth coniferous forests.

In conclusion, the protected area network is highly dependent on the susceptibility of focal habitats to climate change effects. If the focal habitats are expected to change rapidly because of climate change (as with mires and heaths), the protected area network appears more vulnerable in preserving species in the focal habitats than if the time lag in the effects of climate change on habitat is presumed to be long (as with old-growth forests).

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Appendix

Bird species' census data in Finnish protected areas (doi: 10.3897/natureconservation.3.3635.app). File format: MS Word Document (doc).

Explanation note: Mean densities and number of observations of species in 1981–1999 and in 2000–2009.