CrossMark

ORIGINAL PAPER

Long-term decline of southern boreal forest birds: consequence of habitat alteration or climate change?

Raimo Virkkala[1]

Abstract Climate change and habitat degradation due to land use are the key factors threatening biodiversity. It is important to study both the separate and joined effects of climate warming and land use on biodiversity. In this work long-term population changes of southern boreal forest birds were studied in relation to climate change and direct habitat alteration due to forestry. The study was based on annually repeated bird censuses in 23 consecutive years (1993–2015) in a managed forest landscape. Results were compared with population changes in protected areas where logging is not allowed. During the study period, total bird density declined by 18 % with a change in the bird community composition. Out of the 12 most abundant species seven showed a significant negative trend and only one species a positive trend. Population declines could be connected with the direct alteration of habitat as a consequence of forestry or with the effect of climate change in the case of those species which declined also in protected areas. The increased species are abundant across Europe in human-modified habitats. Due to habitat alteration and climate warming, specific characteristics of southern boreal forest bird communities are changing with communities representing a pattern towards global homogenization. Thus, habitat alteration strengthens the negative effects of climate change.

Keywords Boreal · Climate change · Decline · Forest bird · Forestry

✉ Raimo Virkkala
raimo.virkkala@ymparisto.fi

[1] Natural Environment Centre, Finnish Environment Institute, Mechelininkatu 34a, P.O. Box 140, 00251 Helsinki, Finland

 Springer

Introduction

Climate and land use change are the main drivers of biodiversity change (Sala et al. 2000; Travis 2003), and pressures on biodiversity have increased in the early 21st century (Butchart et al. 2010). Climate change and land use change interact in their impact on biodiversity, but their combined effects are still poorly known (Jiguet et al. 2010; Oliver and Morecroft 2014). In a recent study, the speed of climate change was estimated to be an order of magnitude higher than the speed of land use change in most regions of US (Ordonez et al. 2014). In preserving biodiversity it is important to highlight areas most vulnerable to changes due to individual or combined effects of climate and land use change (Ordonez et al. 2014).

Thuiller et al. (2004) suggested that at a coarse resolution variation in land cover is mainly driven by climate, and thus climate variables can effectively account for most of the explanatory power of land cover. However, Luoto et al. (2007) showed that determinants of bird species distributions are hierarchically structured: climatic variables are large-scale determinants followed by land cover at finer resolution. At the large scale, species are restricted by climate variables (see e.g., Root 1988) and occur in a species-specific climate space (Huntley et al. 2007; Araújo and Peterson 2012).

Climate change is a key driver affecting bird assemblages in boreal forests (Huntley et al. 2007; Jetz et al. 2007; Bellard et al. 2012; Jiguet et al. 2013). The boreal forest is the biome where climate is predicted to change most rapidly. In a comparison of the world's 14 main biomes and their respective protected areas, Loarie et al. (2009) showed that climate change by year 2100 was among the most rapid in protected areas of the boreal biome. In a recent study comparing spatial patterns in the abundance of European birds, Howard et al. (2015) showed that the relative importance of climate is higher in boreal northern Europe in Finland and Sweden than in central and southern Europe where land use patterns are relatively more important. For example in Britain, despite more stable land use intensity in recent years, climate change has not overtaken land use intensity as the dominant driver of bird populations (Eglington and Pearce-Higgins 2012).

Species distributions have already been observed to shift polewards (latitudinally) and upwards (altitudinally) in several species groups as a consequence of climate change (see Hickling et al. 2006; Chen et al. 2011; Brommer et al. 2012). In addition to species range shifts, also densities of boreal bird species have shifted northwards. In Finland, for example, the mean weighted latitude of density moved northwards, on average, by 1.3 km year^{-1} from the 1970s to the 2010s (45 km during the study period of 35 years) in the 94 most common land bird species (Virkkala and Lehikoinen 2014). Densities of the most abundant forest bird species distributed over the whole country had also shifted northwards. Virkkala and Rajasärkkä (2011a) showed that populations of southern species had increased by 29 % and northern species declined by 21 % in a set of 96 Finnish protected areas between two time periods, 1981–1999 and 2000–2009. Temporal changes were most pronounced toward species range boundaries: southern birds increased most in northern protected areas and northern species showed the greatest decrease in southern protected areas (Virkkala and Rajasärkkä 2011b). As a consequence of climate change, boreal bird assemblage composition is changing with a time lag of 1–3 year(s) in relation to temperature increase (Lindström et al. 2013).

Another key driver affecting boreal bird species is forestry, i.e. logging and management of forests for the extraction of wood. In NW Europe almost all forest land outside protected areas is subject to systematic silvicultural practices, which include thinning of

young and middle-aged stands, clear-cutting at a stand age of 60–120 years depending on site type and location, and replanting. Compared to naturally-dynamic forest landscapes, logging and management result in even-aged stands and a truncated age-class distribution with a reduced area of old-growth forest. The effects of forestry, thus, differ considerably from those of natural disturbances to which boreal species are evolutionarily adapted, such as fire and storm-felling (see Esseen et al. 1997). In particular, species dependent on dead wood, old-growth and uniform forests with vertically heterogeneous structure suffer from the effects of forestry (Helle and Järvinen 1986; Virkkala 1991; Väisänen et al. 1998; Roberge et al. 2008). The effects of forestry and climate change can also act in parallel. For example, many northern boreal forest species may suffer both from a warming climate and the loss of old-growth forests (e.g., Siberian jay *Perisoreus infaustus*; Edenius et al. (2004); Muukkonen et al. (2012)).

In this paper I study population changes of specific southern boreal forest bird species and changes in bird community over a long time period, based on 23 consecutive years. The study was carried out in a managed forest area where forests were logged continuously. However, there has been a change in the logging practices, as also in the whole of southern Finland, because the earlier harvesting (until the 1970s) of forests was largely based on the removal of individual trees, but clear-cutting with replanting have replaced the earlier logging procedures. The results are compared with population changes in southern Finnish protected areas where logging is not allowed and also with population changes in the whole of Finland to find out whether the population changes are primarily caused by (1) direct habitat alteration (forestry) or by (2) climate change? If population changes in the managed forests parallel those in protected areas then population changes could be caused by climate change. On the other hand, if populations decline in managed
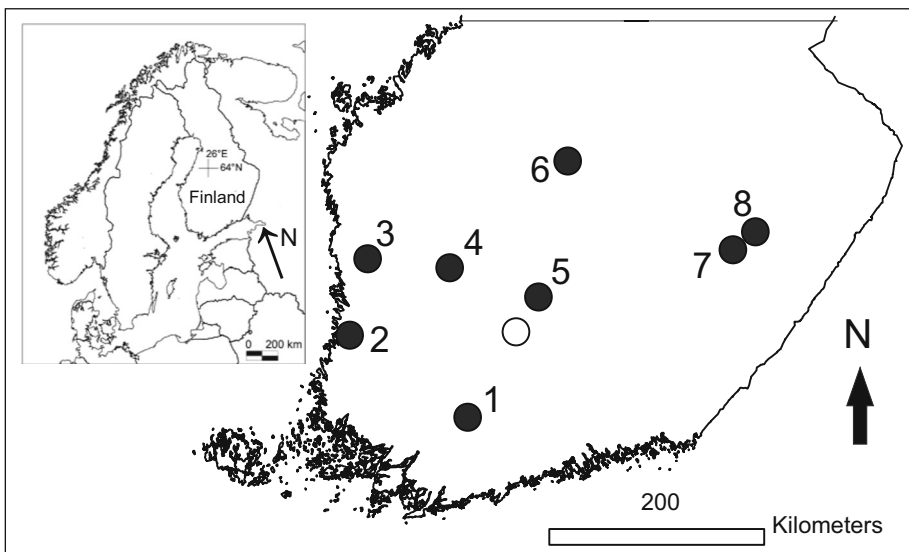

Fig. 1 Location of the study area of managed forests (*open circle*), and the protected areas in southern Finland. *1* Liesjärvi national park, *2* Pinkjärvi protected area, *3* Lauhanvuori national park, *4* Seitseminen national park, *5* Isojärvi national park, *6* Pyhä-Häkki national park, *7* Linnansaari national park, *8* Kolovesi national park

forests, but increase or remain stable in protected areas, direct habitat alteration would probably be the key factor causing the population decline.

Materials and methods

Study area

The study area was situated in a managed forest landscape in southern Finland, in the southern boreal forest vegetation zone (61° 18′ N, 24° 39′ E, Fig. 1). Over 80 % of the land area in the region (318 km^2, former municipality of Luopioinen) is forests (Tomppo et al. (1998), see also Räsänen et al. (2016)), the remainder being mainly agricultural land.
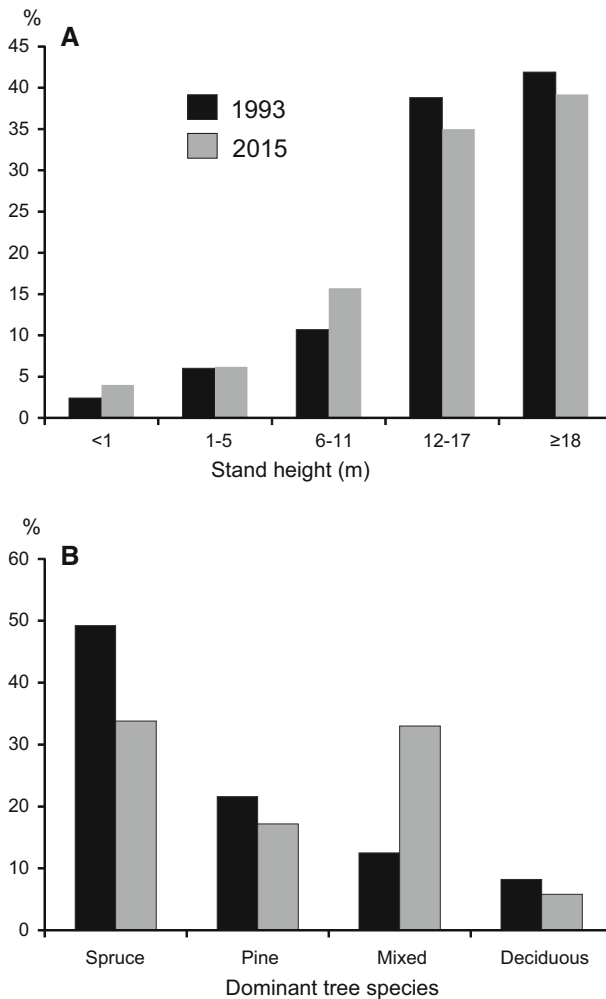

Fig. 2 **a** Stand height of forests (in metres) in the different height classes in the study area in 1993 and in 2015. **b** Dominant tree species in forests (stand height over 5 metres) in 1993 and in 2015

Annual bird censuses were carried out by the author in managed forests in an area of 7 km^2 (Ahvenusmaa—Nivunkulma) between 1993 and 2015. Managed forests in the study area consisted of varying age classes with recent clear-cuts, young saplings, and middle-aged, mature and old-aged stands. Forested area continues outside the study area.

Bird censuses located exactly at the same sites were repeated each year at the turn of May–June by the author. In the main belt (see later) of the transects dominant tree species and their mean stand height were recorded. Four classes were used to determine the dominant tree species: spruce, pine, deciduous trees as well as mixed stands with both coniferous and deciduous trees in equal (about 50 %) proportion. Trees with a height of 1–5 m were recorded as saplings (bushes), 6–11 m as young forests, 12–17 m as middle-aged forests and over 18 m as mature or old-aged forests. In the clear-cuts tree height was <1 m. In climax forest, stands are 18–25 m tall depending on the site type with dry types having the lowest and most productive herb-rich forests types the highest height of stand. There were no nest-boxes available along the transects.

The height of forest stands in different categories in the beginning (1993) and at the end (2015) of the study are presented in Fig. 2a. Although the area was continuously logged by clear-cuts, the average height of the forests had not changed much during the study. The weighted mean of stand height was 14.6 m in 1993 and 14.1 m in 2015. It should be noted that annual growth of young and middle-aged stands is about 0.5 m or even more in productive herb-rich, moist and mesic site types, so that at these site types a forest of 10 m height at the beginning of the study was about 20 m at the end of the study. On the other hand, the proportion of dominant tree species shows a quite different pattern as the proportion of spruce-dominated forests had declined considerably due to logging, from 49 to 33 %, and the proportion of mixed forests had increased from 13 to 33 % (Fig. 2b). Mature and old-aged spruce forests (tree height ≥18 m) declined by one third due to loggings, from 27 to 18 %. Forest patches have also been fragmented (decrease in forest patch size) during the study as a consequence of logging procedures. Most of the clear-cuts (herb-rich,
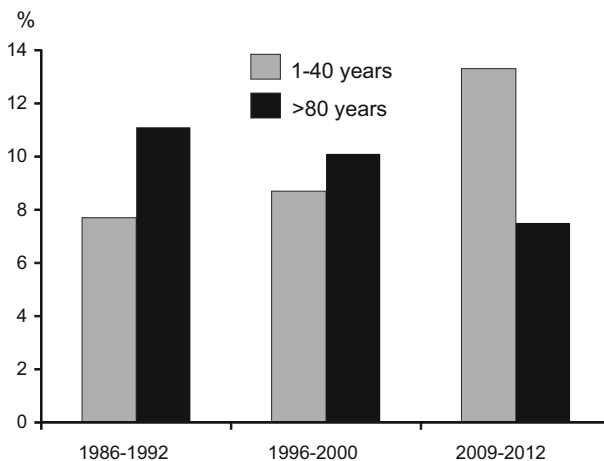

Fig. 3 Proportion of old spruce-dominated forests (stand age over 80 years) and young (stand age of 1–40 years) spruce-dominated forests (including mixed stands of spruce and deciduous trees) in the forest land in southern half of Finland (see Fig. 1) based on National Forest Inventories (NFI) carried out in 1986–1992 (NFI8), in 1996–2000 (NFI9) and in 2009–2012 (NFI11) (Salminen and Salminen 1998; Metinfo 2012)

moist and mesic site types) are planted with spruce, but deciduous trees (mainly birch) increase naturally therein as mixed trees. The dry sites are planted with pine.

Whereas the earlier harvesting of forests in the area was largely based on the removal of individual trees, clear-cutting with replanting increased from the early 1970s onwards. During the study, the commercial regeneration of forests was based on clear-cutting with leaving 5–10 retention trees per hectare (see also Vanha-Majamaa and Jalonen 2001) according to the new silvicultural recommendations. Approximately half of the stand volume is removed in the thinning operations of growing stock, which are being carried out twice or three times during the harvest cycle. The forests in the study area are privately owned.

Same patterns in forest structure as a consequence of forest management and loggings as in the present study area are observable in the whole of southern Finland based on National Forest Inventories (Fig. 3). Old spruce-dominated forests (stand age over 80 years) have declined by 35 % (change of proportion in all forest land from 11.5 to 7.5 %) in southern Finland from 1986–1992 to 2009–2012 (based on Salminen and Salminen 1998; Metinfo 2012). During the same time period, spruce-dominated (including mixed stands of spruce and deciduous trees) young stands of 1–40 years have increased over 70 % (change of proportion in all forest land from 7.7 to 13.3 %) (Salminen and Salminen 1998; Metinfo 2012).

Bird census data

Land birds in the study area were counted using the Finnish line transect census method (Järvinen and Väisänen 1976; Järvinen et al. 1991; Virkkala and Lehikoinen 2014). The line transect method is a one-visit census, in which birds are recorded separately in a 50 m wide main belt and in a supplementary belt outside this. The supplementary belt consists of all birds observed outside the main belt without any distance limit. The main and supplementary belts together comprise the survey belt. The line transect censuses were carried out in the early morning hours (between 3:00 AM and 8:00 AM) when the singing activity of birds is the highest. In line with the instructions of the Finnish line transect census a male heard singing, an otherwise observed male or female, or a group of fledglings were all interpreted as a pair (see Järvinen and Väisänen 1976; Järvinen et al. 1991). If both a male and a female or two alarming individuals (sexes not identifiable) were observed in the same site, they were always interpreted as one pair. In southern Finland, the density estimate of bird species based on a line transect census method is on average approximately 70 % of that based on thorough mapping censuses (Tiainen et al. 1980).

In calculating densities (pairs/km^2), observations of birds in the survey belt were adjusted by applying species-specific correction coefficients, which take into account differences in the observability of species (Järvinen and Väisänen 1983). The species-specific correction coefficient of a given species is based on the ratio of the numbers in the main and supplementary belts. The species-specific correction coefficients provided by Väisänen et al. (1998), Virkkala and Lehikoinen (2014), and Lehikoinen and Virkkala (2015) were used, and were calculated based on large, nation-wide line transect data sets. Since the sample size is relatively small for many species, only the most abundant species and species groups having adequate sample sizes were compared (see Supplementary Material, Table S1).

Censuses were all performed between 28 May and 7 June every year. In years with an early spring the censuses were carried out at the end of May and in cases of a late spring early June. The same four 2-km long transects were repeated each year. All transects

consisted of straight lines with no between-transect overlap in the study area. The distance between the adjacent transects was ca. 0.9 km. All the censuses were carried out by the author.

Results of bird censuses of the study area were compared with the results of bird censuses carried out in eight forested protected areas situated at a distance of c. 200 km from the study area (Fig. 1). The same line transect census method was adopted also in protected areas. These data were part of censuses carried out in the network of protected areas in the whole of Finland and presented in detail in Virkkala and Rajasärkkä (2011a, b, 2012). These data were compared between two periods, 1981–1999 and 2000–2009. In the eight protected areas of the present study, the median census years were 1988 in the first and 2005 in the second period. The mean number of years that censuses were carried out in each protected area was four in 1981–1999 and two in 2000–2009. The same transects were not repeated, but censuses in each protected area included the same proportion of habitats in the two periods. On average, 90 % of the land area of these protected areas was covered by forests, the rest being mires and rocky outcrops. Logging is not allowed in protected areas. The total length of transects in each protected area in both the periods and size of the areas are presented in the Supplementary Material (Table S2).

Statistical analyses

The statistical significance of temporal change (trend) in the total density of all bird pairs and density changes of the most abundant species (at least 2 % of all bird pairs in the community) were studied based on TRIM (Trends & Indices for Monitoring data) to estimate additive slope parameter with standard error (S.E) (Pannekoek and van Strien 2005). The programme TRIM is freely available, and it accounts for over-dispersion and serial autocorrelation using a generalized estimating equation algorithm. TRIM is a standard programme in analysing bird monitoring data sets (see Pannekoek and van Strien 2005). When presenting results in bird densities in 1993–2015, the first year (1993) was given a value of 1.00 with which densities in the other years were compared.

The census results of the eight protected areas were compared pairwise between the two periods (1981–1999 and 2000–2009) and the density difference of each species tested by Wilcoxon signed rank test.

Percentage similarity (PS) of the bird community within the study period was calculated as $PS = \sum \min(p_{1i}, p_{2i})$, where p_{1i} and p_{2i} are proportions of species i in samples 1 and 2. This similarity index is a measure of dissimilarity between two communities (spatially or temporally), based on relative (proportional) abundances of species. Percentage similarity of the bird community were compared here temporally based on mean density in four (three) year periods: 1993–1996, 1997–2000, 2001–2004, 2005–2008, 2009–2012, and 2013–2015.

Species groups

In addition to calculation of annual total density of bird species, bird species were classified based on their migratory status (Supplementary Material, Table S1): resident species, partial migrants, short-distance migrants and long-distance migrants according to Väisänen et al. (1998) and Valkama et al. (2014). Partial migrants include species in which part of the population is resident and part is migratory. Birds having irregular movements were also included in this group. Short-distance migrants overwinter in central and southern

Europe including the Mediterranean region and long-distance migrants in Africa south of
the Sahara or in southern Asia.

Climate variables

Climate change during the study period was investigated by studying changes in the mean
temperature of the whole year as well as of April–June, which is a particularly important
period for breeding birds. These data of climate variables are based on 10×10 km
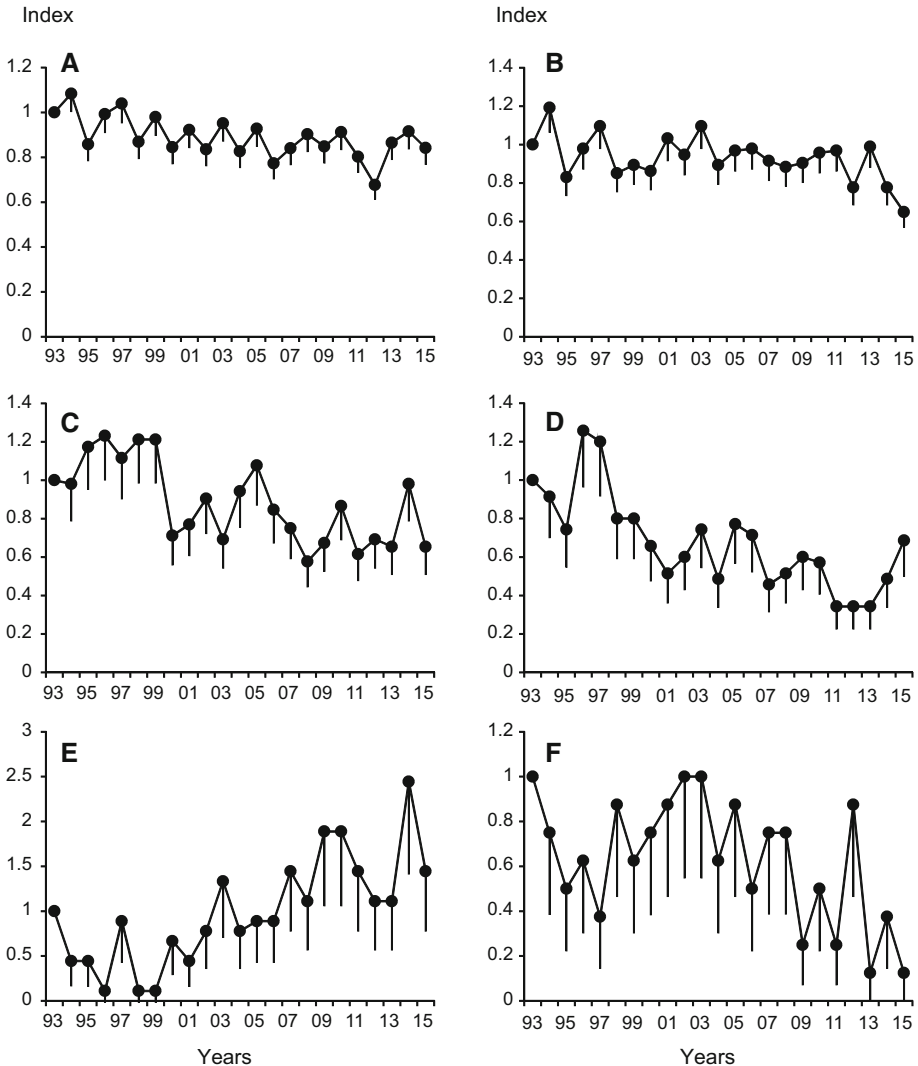

Fig. 4 Density changes of species in 1993–2015 with mean density and S.E. presented yearly. Density in 1993 set as an index of 1. **a** Total density of species, **b** Chaffinch *Fringilla coelebs*, **c** willow warbler *Phylloscopus trochilus*, **d** redwing *Turdus iliacus*, **e** great tit *Parus major*, **f** willow tit *Poecile montanus*

gridded data obtained from the Finnish Meteorological Institute (Tietäväinen et al. 2010). The values of climate variables during the study period were extracted from the 10 × 10 km square, where the study area was located. Mean annual temperature has risen by approximately 1.1 °C (y = 0.050x + 3.958) and mean April–June temperature by approximately 0.9 °C (y = 0.044x + 8.604) in the study area during the study period (in 1993–2014).

Results

Total population density of birds declined on average by 0.89 %/year in 1993–2015 (slope parameter ± standard error = −0.0089 ± 0.0023, P < 0.01) corresponding to a decline of 17.9 % for the whole period (see Fig. 4). Among the most abundant 12 species, 7 declined significantly, one increased and 4 species did not show any significant trend (Table 1). Altogether, short-distance migrants declined by 20.7 %, long-distance migrants by 25.0 % and residents by 29.4 %, whereas partial migrants increased by 2.4 % during the study period (see Supplementary Material, Table S1)).

The four most abundant species of the study, chaffinch *Fringilla coelebs*, willow warbler *Phylloscopus trochilus*, redwing *Turdus iliacus* and goldcrest *Regulus regulus*, all declined significantly with redwing and goldcrest decreasing to less than half (Table 1; Fig. 4). The largest decrease was, however, in the resident willow tit *Poecile montanus*, which declined to less than one third (Table 1; Fig. 4). In contrast, partial migrant great tit *Parus major* (Table 1; Fig. 4), as also blue tit *Cyanistes caeruleus* (slope parameter:

Table 1 Population trends of the 12 most abundant forest bird species (dominance >2 % in the bird community) in 1993–2015

Species	Dominance (%)	Slope parameter	S.E.	P	% Change
Chaffinch *Fringilla coelebs* (S)	22.8	−0.0096	0.0025	<0.01	−19.1
Willow warbler *Phylloscopus trochilus* (L)	10.9	−0.024	0.0047	<0.01	−41.4
Redwing *Turdus iliacus* (S)	6.2	−0.0405	0.0080	<0.01	−59.7
Goldcrest *Regulus regulus* (P)	5.9	−0.0381	0.0061	<0.01	−56.2
Robin *Erithacus rubecula* (S)	5.4	−0.0064	0.0092	n.s.	−13.2
Eurasian Siskin *Carduelis spinus* (P)	4.6	−0.0381	0.0061	<0.01	−57.4
Great tit *Parus major* (P)	3.8	0.0867	0.0167	<0.05	+522.9
Song thrush *Turdus philomelos* (S)	3.7	−0.0113	0.0071	n.s.	−22.1
Spotted flycatcher *Muscicapa striata* (L)	3.4	0.0092	0.0017	n.s.	+22.3
Dunnock *Prunella modularis* (S)	2.6	−0.0013	0.0092	n.s.	−2.8
Willow tit *Poecile montanus* (R)	2.2	−0.0517	0.0178	<0.01	−68.9
Tree pipit *Anthus trivialis* (L)	2.1	−0.0350	0.0102	<0.01	−54.3

The significance (P, n.s. = non-significant) of a trend is based on linear TRIM estimate of additive slope parameter with standard error (S.E) (see Pannekoek and van Strien 2005). The percentage change of the population change for the whole period 1993–2015 is presented

S short-distance migrant, *L* long-distance migrant, *R* resident, *P* partial migrant

0.0918 ± 0.0191, P < 0.05) increased several fold (523 and 590 %, respectively), particularly during the past ten years (see Supplementary Material, Table S1)). The combined density increase of great tit and blue tit largely compensates for the losses of other bird pairs in the latter study period of 2004–2015, when the overall bird pairs declined by only 1.9 % compared with the decline of 15.4 % in 1993–2004. If great tit and blue tit are excluded from the data, the rest of the bird pairs declined by 18.0 % in 1993–2004 and by 9.3 % in 2004–2015. In 2004–2015 great tit was already the third most numerous birds species after chaffinch and willow warbler, and blue tit the ninth most numerous.

In addition, mean density of northern species occurring in the study area at their southern edge of distribution, brambling *Fringilla montifringilla*, redpoll *Carduelis flammea* and rustic bunting *Emberiza rustica*, declined by 70 % from 1993–2003 to 2004–2015.

When percentage similarity of bird community is compared in 4 year periods, the similarity declined gradually over time showing the change in the composition of the community (Table 2). For example, the similarity-index of the community compared with 1993–96 was 91.5 % in 1997–2000 but only 82.0 % in 2013–2015.

When the population changes of the most abundant species in the managed forest area were compared in the protected areas in the nearby regions between 1981–1999 and 2000–2009, five species declined, while seven species did not show any significant change in density (Table 3). The blue tit increased over tenfold (mean density ± S.E.; 1981–1999: 0.1 ± 0.2 pairs/km^2, 2000–2009: 1.7 ± 1.2 p/km^2; $P = 0.018$, Wilcoxon signed rank test), and the combined density of the northern species, brambling, redpoll and rustic bunting, declined by about 80 % (1981–1999: 4.2 ± 1.5 p/km^2, 2000–2009: 0.9 ± 1.0 p/km^2, $P = 0.017$, Wilcoxon signed rank test).

Discussion

The study shows the overall decline of total bird density and the decline of the most abundant bird species with a gradual change in the composition of bird community in southern boreal forest (Solonen 1996; Virkkala 2004; Vihervaara et al. 2015). The results are in line with Pan-European population changes of birds. Inger et al. (2015) showed using a 30-year dataset of 144 bird species that the overall avian abundance is declining with most of the decline being attributed to common and small-sized species. In Europe, common forest birds declined by 13 %, and common forest specialists by 18 % in a 23-year period of 1980–2003 (Gregory et al. 2007), as also in the present 22-year study (18 %). Particularly the decrease of long-distance migrants and residents have been

Table 2 Percentage similarity of forest bird community in 1993–2015 based on four (three in 2013–2015) year periods

Years	Years				
	1993–1996	1997–2000	2001–2004	2005–2008	2009–2012
1997–2000	91.5				
2001–2004	87.9	84.9			
2005–2008	88.1	84.2	89.0		
2009–2012	83.9	80.2	88.2	88.1	
2013–2015	82.0	79.3	82.7	84.7	87.1

Table 3 Population densities (pairs/km^2, mean $\pm$ standard error) of the 12 studied species in forested protected areas (N = 8) in the nearby regions based on censuses carried out in 1981–1999 and in 2000–2009

Species	Years		
	1981–1999	2000–2009	P
Chaffinch *Fringilla coelebs*	54.8 $\pm$ 5.3	53.8 $\pm$ 7.6	0.674
Willow warbler *Phylloscopus trochilus*	33.2 $\pm$ 3.8	16.1 $\pm$ 5.8	0.017
Redwing *Turdus iliacus*	4.9 $\pm$ 1.3	2.9 $\pm$ 1.0	0.036
Goldcrest *Regulus regulus*	7.4 $\pm$ 1.2	7.6 $\pm$ 1.4	0.726
Robin *Erithacus rubecula*	7.0 $\pm$ 1.3	7.7 $\pm$ 1.3	0.779
Eurasian Siskin *Carduelis spinus*	8.8 $\pm$ 1.0	8.3 $\pm$ 1.3	0.263
Great tit *Parus major*	6.0 $\pm$ 0.8	7.2 $\pm$ 1.1	0.484
Song thrush *Turdus philomelos*	4.0 $\pm$ 0.4	3.8 $\pm$ 0.8	0.624
Spotted flycatcher *Muscicapa striata*	15.0 $\pm$ 1.3	9.4 $\pm$ 1.7	0.017
Dunnock *Prunella modularis*	2.3 $\pm$ 0.6	1.6 $\pm$ 0.5	0.161
Willow tit *Poecile montanus*	4.1 $\pm$ 0.6	2.1 $\pm$ 0.2	0.012
Tree pipit *Anthus trivialis*	12.0 $\pm$ 0.8	7.3 $\pm$ 1.7	0.017

Statistical testing based on paired Wilcoxon signed rank -test

observed both at the European (Gregory et al. 2007) and at the national level (Laaksonen and Lehikoinen 2013; Fraixedas et al. 2015a).

The decline of bird species can be explained largely by the effects of climate change or habitat alteration or by combined effects of these factors. In order to separate direct habitat alteration from indirect climate change effect, knowledge of population changes in protected areas, where logging is not allowed, is highly essential. Of the declined species in the present study, willow warbler, redwing, willow tit and tree pipit also declined in the protected areas. The other declined species, chaffinch, goldcrest and siskin did not show any temporal change in density in the protected areas. In addition, according to Laaksonen and Lehikoinen (2013) who studied population changes of bird species in the whole of Finland, all of the species which declined in the managed forests of the present study also showed a decline in density in Finland in 2000–2012. Fraixedas et al. (2015b) studied population trends of 32 common forest bird species in southern Finland, and also they found the decline of the same species as in the present study.

The declined willow warbler and redwing prefer young, mixed stands with bushy vegetation, forests dominated by deciduous trees and forest edges (Tiainen et al. 1983; Helle 1985; Virkkala 1987). Thus, these species should even have benefited from the logging of old spruce-dominated forests that caused an increase of young, mixed stands during the study years (see Virkkala 1987). The population changes of these species are most likely connected with climate change effects, as the mean weighted density of these species have also moved considerably towards the north in Finland from the 1970s to the 2010s thus following climate change (Virkkala and Lehikoinen 2014; Lehikoinen and Virkkala 2015). These species have also declined in protected areas. Climate change causes species abundances and ranges to shift northwards, having probably resulted, for example, in the decrease of northern species (Laaksonen and Lehikoinen (2013); see also Brommer et al. (2012); Virkkala et al. (2014)). Moreover, redwing has declined in large areas in Europe, so that it is regarded as a Red-Listed Species both in the EU (vulnerable) and in the whole of Europe (near-threatened, (BirdLife International 2015). The largest

European populations of both redwing and willow warbler are in northern Europe (Bird-Life International 2004).

In addition, also the tree pipit declined both in the protected areas and in the managed forest area, although logging of old, closed spruce forests created more suitable habitat of open, light forests for the species (e.g., Väisänen et al. 1998). Tree pipit and willow warbler are long-distance migrants overwintering in Africa, and thus are affected by climate change globally, as also by land use in the wintering areas and in the stop-over sites.

On the other hand, chaffinch, goldcrest and siskin prefer spruce-dominated forests (Tiainen et al. 1983; Hanski and Haila 1988; Solonen 1996; Virkkala 2004), and, thus, the logging of old spruce forests has a negative effect on these species. Siskin is a spruce seed eater (see Hagemeijer and Blair 1997; Virkkala 2004) and therefore directly affected by the logging of old spruce forests. In their study of the chaffinch Hanski and Haila (1988) observed, based on radio-tracking of individuals, that old spruce-dominated forests were almost completely occupied each year, whereas variation in the occupancy of pine-dominated forests was greater. Moreover, old spruce forests have declined in southern Finland as a consequence of logging, which has been observed to affect, for example, the decline of the Siberian jay preferring old-growth forests (Muukkonen et al. 2012).

In addition, the resident willow tit suffers from the effects of forestry (Virkkala 2004) such as reduced wintering habitat and carrying capacity of its territory (Siffczyk et al. 2003). In the willow tit both nest and adult survival have been observed to decline when the understory spruce density is reduced as a consequence of thinning of coniferous forest (Eggers and Low 2014). Thus, the density changes of the willow tit can be explained by combined effects of direct habitat alteration and climate change, as the species also declined in protected forests not affected by logging procedures. The mean weighted density of the willow tit has also moved considerably towards the north in Finland from the 1970s to the 2010s (Lehikoinen and Virkkala 2015).

Logging procedures carried out in the study area are similar to, not only elsewhere in Finland, but also across the boreal countries in the northwestern Europe that all apply even-aged stand management: thinning, clear-cut harvesting and replanting (Kuuluvainen et al. 2012). Therefore the effects of forestry on bird populations can quite likely be generalized over large areas. For example the willow tit, negatively affected by logging procedures, is a declining species in the whole of Europe with populations having declined in the European countries in the long term (1980–2013) by 69 % and in the short term (2004–2013) by 33 % (European Bird Census Council 2015). As a consequence, willow tit is listed as vulnerable in the EU (BirdLife International 2015). The largest willow tit populations in the EU reside in Finland and in Sweden (European Union 2015).

Among the most abundant species in 1993–2015, the numbers of great tits increased significantly. In addition, the rapidly increased blue tit was already during the last study years among the most abundant species in the bird community. The increased species, great tit and blue tit share similar ecological properties. They both are partial migrants and benefit from the increased food supply provided by humans during winters (Väisänen 2008; Fraixedas et al. 2015a). Furthermore, they are typical southern species for which climate warming, such as milder winters, is clearly favourable. Blue tit has increased considerably in the protected areas in the nearby regions and both species have increased in the protected area network in the whole country (Virkkala and Rajasärkkä 2011b). The species benefit from the forestry-driven change of spruce- and pine-dominated forests to mixed stands. In contrast with the year-round residents, willow tit and crested tit *Lophophanes cristatus*, overwintering great tit and blue tit individuals typically move from the forest to human settlements during winter. Moreover, great tit and blue tit breed in nest-

boxes that are commonly provided nowadays and can breed in nest holes in the retained aspens in the clear cuts (Carlson 1994). In contrast, willow tit and crested tit excavate their nesting cavities in decaying birch stumps, which are often destroyed during logging procedures (Hautala et al. 2004; Rabinowitsch-Jokinen and Vanha-Majamaa 2010). A recent Swedish study on species breeding in cavities showed that great tit and blue tit could adjust to increasing temperatures while the migrant species pied flycatcher *Ficedula hypoleuca* could not, leading progressively to the exclusion of the pied flycatcher from the area (Wittwer et al. 2015).

In northern Finland, Virkkala (1987, 1991) found, based on studies carried out in the 1980s, that the total density of bird pairs did not differ between virgin, old-growth pine-dominated forests and managed pine-dominated forests, or between uniform spruce-dominated and fragmented spruce-dominated forests. Although northern taiga species preferring old-growth forests declined in managed and fragmented forests, willow warbler and redwing increased in these forests (see also Helle and Järvinen 1986) and compensated for the losses caused by forestry in the total density of the bird community. Thus, the positive effects of logging on total bird density via increase of willow warbler and redwing seem not to prevail any more in a changing climate.

The present study shows that boreal forest bird communities are changing gradually towards communities that resemble those of the present-day central European temperate forests (Jiguet et al. 2010; Lindström et al. 2013). Great tit and blue tit are abundant across Europe in human-modified habitats. Their increase among the most abundant species in southern boreal forests shows the pattern of global homogenization i.e. communities located far away resemble each other more with the same species dominating (e.g., Olden 2006). Thus, the specific characteristics of bird communities in southern boreal forests may largely disappear as a consequence of both direct habitat alteration, such as logging procedures, and climate warming.

An important issue here is that forest management favours species benefitting from climate change so that direct habitat alteration is connected with the indirect effects of climate change (Felton et al. 2014; Fraixedas et al. 2015b). Moreover, the overall bird density in southern boreal forests is not increasing but decreasing, which is quite surprising since population densities in temperate forests are much higher than those in boreal forests. This may be due to different patterns of density and range shift (Virkkala and Lehikoinen 2014). It is commonly known that range shifts in the leading edges of species distribution areas have been much larger than those in the trailing edges (see Jump et al. 2009). However, when studying abundance shifts of southern and northern boreal bird species the situation is the opposite: southern species have advanced less than the northern species have retreated (Virkkala and Lehikoinen 2014). This kind of asymmetric pattern may cause a decline in the total density of a bird community in a given area, particularly when the habitat quality is deteriorated for many species due to intensive forestry practices.

Concluding remarks

The present study shows that both direct habitat alteration and climate change are affecting bird species both separately and jointly. However, habitat alteration strengthens the negative effects of climate change. Therefore, the protected area network is highly important in preserving biodiversity in boreal forests by alleviating the negative effects of both habitat alteration and climate change (Virkkala et al. 2014).

References

Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling. Ecology 93:1527–1539. doi:10.1890/11-1930.1

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377. doi:10.1111/j.1461-0248.2011.01736.x

BirdLife International (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge

BirdLife International (2015) European Red List of Birds. Office for Official Publications of the European Communities, Luxembourg

Brommer JE, Lehikoinen A, Valkama J (2012) The breeding ranges of Central European and arctic bird species move poleward. Plos One 7(9):e43648. doi:10.1371/journal.pone.0043648

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié JC, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168. doi:10.1126/science.1187512

Carlson A (1994) Cavity breeding birds and clearcuts. Ornis Fenn 71:120–122

Chen I-C, Hill JK, Ohleműller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026. doi:10.1126/science.1206432

Edenius L, Brodin T, White N (2004) Occurrence of Siberian jay *Perisoreus infaustus* in relation to amount of old forest at landscape and home range scales. Ecol Bull 51:241–247

Eggers S, Low M (2014) Differential demographic responses of sympatric Parids to vegetation management in boreal forest. For Ecol Manag 319:169–175. doi:10.1016/j.foreco.2014.02.019

Eglington SM, Pearce-Higgins JW (2012) Disentangling the relative importance of changes in climate and land-use intensity in driving recent bird population trends. Plos One 7(3):e30407. doi:10.1371/journal.pone.0030407

Esseen P-A, Ehnström B, Ericson L, Sjöberg K (1997) Boreal forests. Ecol Bull 46:16–47

European Bird Census Council E (2015) Trends of common birds in Europe, 2015 update. http://www.ebcc.info/index.php?ID=587. Cited Sep 26, 2015

European Union (2015) Bird Directive article 12 reporting. Willow Tit: http://bd.eionet.europa.eu/article12/summary?period=1&subject=A238. Cited 26 September, 2015

Felton A, Lindbladh M, Elmberg J, Felton AM, Andersson E, Sekercioglu CH, Collingham Y, Huntley B (2014) Projecting impacts of anthropogenic climatic change on the bird communities of southern Swedish spruce monocultures: will the species poor get poorer? Ornis Fenn 91:1–13

Fraixedas S, Lehikoinen A, Lindén A (2015a) Impacts of climate and land-use change on wintering bird populations in Finland. J Avian Biol 46:63–72. doi:10.1111/jav.00441

Fraixedas S, Lindén A, Lehikoinen A (2015b) Population trends of common breeding forest birds in southern Finland are consistent with trends in forest management and climate change. Ornis Fenn 92:187–203

Gregory RD, Vořišek P, Van Strien A, Meyling AWG, Jiguet F, Fornasari L, Reif J, Chylarecki P, Burfield IJ (2007) Population trends of widespread woodland birds in Europe. Ibis 149:78–97. doi:10.1111/j.1474-919X.2007.00698.x

Hagemeijer WJM, Blair MJ (eds) (1997) The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. T & A D Poyser, London

Hanski IK, Haila Y (1988) Singing territories and home ranges of breeding chaffinches: visual observation vs radio-tracking. Ornis Fenn 65:97–103

Hautala H, Jalonen J, Laaka-Lindberg S, Vanha-Majamaa I (2004) Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biodivers Conserv 13:1541–1554. doi:10.1023/B:BIOC.0000021327.43783.a9

Helle P (1985) Habitat selection of breeding birds in relation to forest succession in Northeastern Finland. Ornis Fenn 62:113–123

Helle P, Järvinen O (1986) Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. Oikos 46:107–115

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Glob Change Biol 12:450–455. doi:10.1111/j.1365-2486.2006.01116.x

Howard C, Stephens PA, Pearce-Higgins JW, Gregory RD, Willis SG (2015) The drivers of avian abundance. patterns in the realtive importance of climate and land use. Glob Ecol Biogeogr 24:1249–1260. doi:10.1111/geb.12377

Huntley B, Green RE, Collingham YC, Willis SG (2007) A climatic atlas of European breeding birds. Durham University, The RSPB and Lynx Edicions, Barcelona

Inger R, Gregory R, Duffy JP, Stott I, Voříšek Petr, Gaston KJ (2015) Common European birds are declining rapidly while less abundant species' numbers are rising. Ecol Lett 18:28–36. doi:10.1111/ele.12387

Järvinen O, Väisänen RA (1976) Finnish line transect censuses. Ornis Fenn 53:115–118

Järvinen O, Väisänen RA (1983) Correction coefficients for line transect censuses of breeding birds. Ornis Fenn 60:97–104

Järvinen O, Koskimies P, Väisänen RA (1991) Line transect census of breeding land birds. In: Koskimies P, Väisänen RA (eds) Monitoring bird populations: a manual of methods applied in Finland. Zoological Museum, Finnish Museum of Natural History, University of Helsinki, Helsinki, pp 33–40

Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. Plos Biol 5:1211–1219. doi:10.1371/journal.pbio.0050157

Jiguet F, Gregory RD, Devictor V, Green RE, Voříšek P, Van Strien A, Couvet D (2010) Population trends of European common birds are predicted by characteristics of their climatic niche. Glob Change Biol 16:497–505. doi:10.1111/j.1365-2486.2009.01963.x

Jiguet F, Barbet-Massin M, Devictor V, Jonzen N, Lindström Å (2013) Current population trends mirror forecasted changes in climatic suitability for Swedish breeding birds. Bird Study 60:60–66. doi:10.1080/00063657.2012.733337

Jump AS, Mátyás C, Peñuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol Evol 24:694–701. doi:10.1016/j.tree.2009.06.007

Kuuluvainen T, Tahvonen O, Aakala T (2012) Even-aged and uneven-aged forest management in boreal fennoscandia: a review. Ambio 41:720–737. doi:10.1007/s13280-012-0289-y

Laaksonen T, Lehikoinen A (2013) Population trends in boreal birds: continuing declines in agricultural, northern, and long-distance migrant species. Biol Conserv 168:99–107. doi:10.1016/j.biocon.2013.09.007

Lehikoinen A, Virkkala R (2015) North by northwest: climate change and directions of density shifts in birds. Glob Change Biol. doi:10.1111/gcb.13150

Lindström Å, Green M, Paulson G, Smith HG, Devictor V (2013) Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. Ecography 36:313–322. doi:10.1111/j.1600-0587.2012.07799.x

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. Nature 462:1052–1055. doi:10.1038/nature08649

Luoto M, Virkkala R, Heikkinen RK (2007) The role of land cover in bioclimatic models depends on spatial resolution. Glob Ecol Biogeogr 16:34–42. doi:10.1111/j.1466-822x.2006.00262.x

Metinfo (2012) Valtakunnan metsien inventointi. Metsävarat metsäkeskuksittain—inventointien VMI9–VMI11 tuloksia. Metla. (http://www.metla.fi/metinfo/vmi/index.htm)

Muukkonen P, Angervuori A, Virtanen T, Kuparinen A, Merilä J (2012) Loss and fragmentation of Siberian jay (Perisoreus infaustus) habitats. Boreal Environ Res 17:59–71

Olden JD (2006) Biotic homogenization: a new research agenda for conservation biogeography. J Biogeogr 33:2027–2039. doi:10.1111/j.1365-2699.2006.01572.x

Oliver TH, Morecroft MD (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. Wiley Interdiscip Rev-Clim Change 5:317–335. doi:10.1002/wcc.271

Ordonez A, Martinuzzi S, Radelo VC, Williams JW (2014) Combined speeds of climate and land-use change of the conterminous US until 2050. Nat Clim Change 4:811–816. doi:10.1038/nclimate2337

Pannekoek J, van Strien A (2005) TRIM 3 manual (trends & indices for monitoring data). Statistics Netherlands, Voorburg

Rabinowitsch-Jokinen R, Vanha-Majamaa I (2010) Immediate effects of logging, mounding and removal of logging residues and stumps on coarse woody debris in managed boreal norway spruce stands. Silva Fenn 44:51–62. doi:10.14214/sf.162

Räsänen A, Kuitunen M, Hjort J, Vaso A, Kuitunen T, Lensu A (2016) The role of landscape, topography, and geodiversity in explaining vascular plant species richness in a fragmented landscape. Boreal Environ Res 21, In press

Roberge J-M, Angelstam P, Villard M-A (2008) Specialised woodpeckers and naturalness in hemiboreal forests—deriving quantitative targets for conservation planning. Biol Conserv 141:997–1012. doi:10.1016/j.biocon.2008.01.010

Root T (1988) Energy constraints on avian distributions and abundances. Ecology 69:330–339

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. doi:10.1126/science.287.5459.1770

Salminen S, Salminen O (1998) Forest resources in Middle Finland, 1988–92, and in South Finland, 1986–92 (In Finnish with an English summary). Metsäntutkimuslaitoksen Tiedonantoja 710:1–137

Siffczyk C, Brotons L, Kangas K, Orell M (2003) Home range size of willow tits: a response to winter habitat loss. Oecologia 136:635–642. doi:10.1007/s00442-003-1256-x

Solonen T (1996) Patterns and variations in the structure of forest bird communities in southern Finland. Ornis Fenn 73:12–26

Thuiller W, Araújo MB, Lavorel S (2004) Do we need land-cover data to model species distributions in Europe? J Biogeogr 31:353–361

Tiainen J, Martin J-L, Pakkala T, Piiroinen J, Solonen T, Vickholm M, Virolainen E (1980) Efficiency of the line transect and point count methods in a south Finnish forest area. In: Proceedings of the VI International Conference on Bird Census Work, Göttingen

Tiainen J, Vickholm M, Pakkala T, Piiroinen J, Virolainen E (1983) The habitat and spatial relations of breeding *Phylloscopus* warblers and the goldcrest Regulus regulus in southern Finland. Ann Zool Fenn 20:1–12

Tietäväinen H, Tuomenvirta H, Venäläinen A (2010) Annual and seasonal mean temperatures in Finland during the last 160 years based on gridded temperature data. Int J Climatol 30:2247–2256. doi:10.1002/joc.2046

Tomppo E, Katila M, Moilanen J, Mäkelä H, Peräsaari J (1998) Kunnittaiset metsävarat, 1990-1994. Metsätieteen Aikak—Folia For 4B(1998):619–839

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc R Soc Lond Ser B-Biol Sci 270:467–473. doi:10.1098/rspb.2002.2246

Väisänen RA (2008) Changes in frequency and abundance of 63 bird species at winter feeding sites in Finland during 19 winters 1988/1989–2006/2007 (In Finnish with English summary). Linnut-vuosikirja 2007:60–79

Väisänen RA, Lammi E, Koskimies P (1998) Distribution, numbers and population changes of Finnish breeding birds (In Finnish with an English summary). Otava, Helsinki

Valkama J, Saurola P, Lehikoinen A, Lehikoinen E, Piha M, Sola P, Velmala W (2014) The Finnish bird ringing atlas, vol. II. Finnish Museum of Natural History and Ministry of Environment, Helsinki

Vanha-Majamaa I, Jalonen J (2001) Green tree retention in Fennoscandian forestry. Scand J For Res Suppl 3:79–90

Vihervaara P, Mononen L, Auvinen A-P, Virkkala R, Lü Y, Pippuri I, Packalen P, Valbuena R, Valkama J (2015) How to integrate remotely sensed data and biodiversity for ecosystem assessments at landscape scale. Landsc Ecol 30:501–516. doi:10.1007/s10980-014-0137-5

Virkkala R (1987) Effects of forest management on birds breeding in northern Finland. Ann Zool Fenn 24:281–294

Virkkala R (1991) Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. Oikos 62:59–66. doi:10.2307/3545446

Virkkala R (2004) Bird species dynamics in a managed southern boreal forest in Finland. For Ecol Manag 195:151–163. doi:10.1016/j.foreco.2004.02.037

Virkkala R, Lehikoinen A (2014) Patterns of climate-induced density shifts of species: poleward shifs faster in northern boreal birds than in southern birds. Glob Change Biol 20:2995–3003. doi:10.1111/gcb.12573

Virkkala R, Rajasärkkä A (2011a) Climate change affects populations of northern birds in boreal protected areas. Biol Lett 7:395–398. doi:10.1098/rsbl2010.1052

Virkkala R, Rajasärkkä A (2011b) Northward density shift of bird species in boreal protected areas due to climate change. Boreal Environ Res 16(B):2–13

Virkkala R, Rajasärkkä A (2012) Preserving species populations in the boreal zone in a changing climate: contrasting trends of bird species groups in a protected area network. Nat Conserv 3:1–20. doi:10.3897/natureconservation.3.3635

Virkkala R, Pöyry J, Heikkinen RK, Lehikoinen A, Valkama J (2014) Protected areas alleviate climate change effects on northern bird species of conservation concern. Ecol Evol 4:2991–3003. doi:10.1002/ece3.1162

Wittwer T, O'Hara RB, Caplat P, Hickler T, Smith HG (2015) Long-term population dynamics of a migrant bird suggests interaction of climate change and competition with resident species. Oikos 124:1151–1159. doi:10.1111/oik.01559