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# Population trends of common breeding forest birds in southern Finland are consistent with trends in forest management and climate change

Sara Fraixedas*, Andreas Lindén & Aleksi Lehikoinen

*S. Fraixedas, A. Lehikoinen, The Helsinki Lab of Ornithology (HelLO), Finnish Museum of Natural History, University of Helsinki, Finland. * Corresponding author's e-mail: sara.fraixedas@helsinki.fi*
*A. Lindén, Aronia Coastal Zone Research Team, Åbo Akademi University and Novia University of Applied Sciences, Ekenäs, Finland*

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In Finland, modern forestry has caused the gross modification of native forest habitats and a loss of biological diversity due to intensive management regimes. Although less than 1% of the old-growth forest area remains in southern Finland, the effects of forestry on bird population long-term trends have not been comprehensively studied in this area. To fill this knowledge gap, we analysed 30 years of monitoring data of 32 common forest breeders in southern Finland. For each species, we fitted piecewise log-linear trends in two segments: 1984–1998 (period 1) and 1999–2013 (period 2). The estimated trends were analysed in relation to the species-specific habitat preferences, average tree height preference, migratory strategy, and latitudinal distribution. The trends turned on average more negative in period 2 compared to period 1, but the between-species variation in this change was not explained by any of the predictors. For the whole study period, species with a preference for late successional and nutrient-poor habitats (mostly found in northern latitudes) showed more negative population trends. In addition, trends changed on average –3% / 500 km latitude. We further developed three summarizing multi-species indices, most of which should be useful for monitoring the general state of breeding forest bird communities in southern Finland. Our results suggest that bird communities are shaped by both a loss of mature forests and by climate warming. The decline of birds preferring native forests, reflected by the mature forest index, could undoubtedly change with an improvement of the conservation effectiveness in southern Finland.

## 1. Introduction

Recent changes in bird numbers have been linked to shifts in species' distributions induced by climate change, both in winter (Maclean *et al.* 2008, Lehikoinen *et al.* 2013a) and during the breeding season (Jiguet *et al.* 2010a, b, Lindström *et al.* 2013). However, the effects of land-use practices sometimes exceed those of climate change in certain habitats (e.g., UK farmlands; Eglington & Pearce-Higgins 2012). In Fennoscandian boreal forests, many studies have focused on the effects of forest management on bird communities (e.g., Edenius & Elmberg 1996), and some management strategies related to Fennoscandian forestry have been assessed as alternatives to clear-cutting to determine the value to bird fauna (e.g., retention of forest strips; Hågvar & Bækken 2005). Modern large-scale forestry was developed following the Second World War, and in Finland its effects on birds were addressed at the end of the 1970s. For example, Järvinen *et al.* (1977) investigated how modern forestry was affecting breeding bird numbers, and later studies focused on the species occurring in northern Finland (e.g., Järvinen & Väisänen 1978, Helle & Järvinen 1986, Virkkala 1987), where forest areas have been strongly altered since the 1950s. More recent literature on boreal bird communities has concluded that most responses may be attributed to the loss of native habitats because of intensified forestry (Schmiegelow & Mönkkönen 2002, Kuuluvainen 2009).

In general terms, trends from the 1940s (first forest bird population estimates for Finland) until the 1990s indicate an increase in the populations of common generalist species and a decline of the specialist ones (Schmiegelow & Mönkkönen 2002). Populations of species strongly dependent on old-growth forests, like the Three-toed Woodpecker (*Picoides tridactylus*), Siberian Tit (*Parus cinctus*) and Siberian Jay (*Perisoreus infaustus*), have shown general declines in northern Finland (Helle 1985, Väisänen *et al*. 1986, Virkkala 1991). Although some results for northern Finland have demonstrated an equal rate of increases and decreases in forest species (Haila & Järvinen 1990), the effects of forest management on trends for southern Finland have been less studied (see for instance Virkkala 2004), and research has mainly focussed on protected areas (e.g., Virkkala *et al.* 1994, Virkkala & Rajasärkkä 2012). In this region, the percentage of old-growth forests is no more than 1%, and the amount of dead wood in managed forests and nature conservation areas only makes up around 37% of that in northern Finland (3.3 $m^3$ / ha in the south and 9.0 $m^3$ / ha in the north) (Virkkala *et al.* 2000, Parviainen & Västilä 2012). Furthermore, the most drastic changes in the forest age structure since the 1960s have been the loss of age classes from 61–100 years, whereas younger age classes have clearly increased (Parviainen & Västilä 2012). Our study concerns common forest species, the vast majority of them found in mature forests. Here, the term "mature" encompasses semi-mature to mature forest age classes (i.e., excluding young-growth stands).

According to Helle and Järvinen (1986), an important driver of the population changes in bird species (at least for northern Finland) may be changes in the availability of their "preferred" habitats (habitats of highest density). Examples include requirements of large enough areas of suitable habitat, association with old-growth forests, and dependence on decaying wood for foraging (Schmiegelow & Mönkkönen 2002). Such specific requirements have been found especially among resident species, for which trends have been declining the most, possibly because they remain year-round in the same forest habitats (e.g., in gallinaceous birds; Hildén 1987). However, the exact mechanisms of population declines are frequently unknown and declines are often steeper than expected by the loss of species' preferred habitats alone, suggesting that other factors, such as climate change together with habitat changes, may also be involved (Niemi *et al.* 1998). Studying how these factors relate to bird trends may shed light on the effects of forest management practices and climate change in southern Finland (Helle & Järvinen 1986). This might allow an evaluation of the conservation status of forest bird species, which goes in line with ongoing conservation programmes (such as METSO, the Forest Biodiversity Programme for southern Finland) applied in the study area. The METSO programme has promoted voluntary forest conservation among private forest owners (over 75% of the southern Finnish forests are privately owned) since its implementation in 2008 (Finnish Government 2008, Syrjänen & Paloniemi 2010, Vihervaara *et al.* 2011).

Forests in the region of southern Finland have experienced and will continue to experience several changes that may affect species' population trends. Some examples are the decline of mature forests (Parviainen & Västilä 2012), as well as the predicted increase in both forest productivity and the proportion of broadleaf trees in primarily coniferous forests as a response to climate change (Kellomäki *et al*. 2005). The importance of investigating patterns of population change, along with the construction of multi-species annual indices,

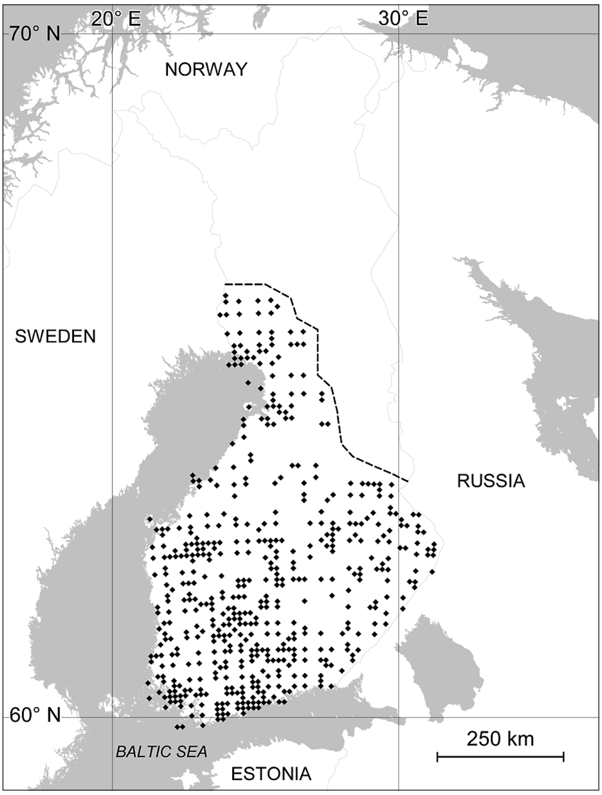

Fig. 1. Distribution of the line transects and point-count routes (from 1984 to 2013) in 10 × 10 km grids. The black dashed line denotes the northern limit of the study area.

relies on the detection and monitoring of the state of communities, and the identification of drivers of community-level changes (e.g., Fraixedas *et al.* 2015).

In this study, we analyse patterns of population change in breeding forest birds in southern Finland and relate them to species' habitat preferences and traits as follows: i) their occurrence in different habitat types; ii) average tree height preferred (as a measure of forest age); iii) the average latitudinal distribution where the species are found; and iv) migratory strategy. Due to the increase in forest productivity and the broadleaf component, first we predicted that species preferring nutrient-rich habitats would show more positive population trends than species preferring nutrient-poor habitats (favouring conifers). Second, due to the loss of mature forests, we expected species preferring old stands to have more negative trends than species preferring young stands. Third, given that species' ranges are moving northwards (Kujala *et al.* 2011, 2013, Virkkala & Rajasärkkä 2011, Brommer *et al.* 2012), we expected that southern species would show more positive population trends relative to northern species. Fourth, the populations of both residents and long-distance migrants have declined over the last few decades (e.g., Hildén 1987, Gregory *et al.* 2007, Laaksonen & Lehikoinen 2013). Therefore, we expected residents, which are present all year-round in their breeding territories, and long-distance migrants, whose populations in Europe seem to face problems along the flyway and in wintering grounds (e.g., Sanderson *et al.* 2006, Vickery *et al.* 2014), to show more negative population trends than short-distance migrants. To facilitate monitoring of the observed patterns, we develop three multi-species indices that summarize the general state of forest breeding bird communities in southern Finland.

## 2. Material and methods

### 2.1. Study area and data collection

The study area covers approximately 23 million ha and the borders were selected according to the goals of METSO – see above (Fig. 1).

We included data from two long-term breeding bird monitoring schemes, both coordinated by the Finnish Museum of Natural History with the data contributed by volunteers. Estimates of the annual abundances of breeding bird species were based on line-transect censuses and point-count routes from the time period 1984–2013. Pairs of birds were used as the census unit; these are based on specific criteria including single individuals, groups of fledglings, nests, and flocks of early-breeding species (Koskimies & Väisänen 1991).

The first scheme was the line-transect censuses of landbirds which have been performed since 1975. Transects are walked once during the breeding season, with census dates ranging from 1st–17th of June for southern and central Finland, and from 10th–30th of June in northern Finland (Koskimies & Väisänen 1991). Differences in census dates are explained by later breeding phenology in northern latitudes (Virkkala & Lehikoinen 2014). Along the line-transect routes, which are approximately six km long each, birds are recorded according to their distance to the transect line. Two distance belts are distinguished: the main belt (25 + 25 m wide), and the supplementary belt, including pairs observed > 25 m from the route and all flying individuals (Koskimies & Väisänen 1991, Laaksonen & Lehikoinen 2013). Habitat data has been recorded from the main belt since 1986, including habitats of the counted birds as well as the amount of habitat along the routes. This information is structured in twelve land-cover categories: a) spruce, b) pine, c) mixed (broadleaf-conifer stands), and d) broadleaf forests, e) bushes (tree height < 5 m, except for mountain birch forests), f) clear-cuts, g) pine mires, h) open mires), i) arable land, j) settlements, k) mountain areas, and l) other. Few birds fall into the last category, which contains habitats such as industrial land and parking areas (Koskimies & Väisänen 1991). For the purpose of this study, categories *a–g* were all considered as forestland, as they are related to different stages of forest succession, even if some of them may actually not comprise forest. Additionally, estimates of the average tree height or average size for open areas are also recorded. Tree height is estimated on an interval scale with a precision of 5 m (and 5 m interval width), comprising six different height classes with mid-points from 5 to 30 m (min 2.5–7.5; max 27.5–32.5).

The second scheme is the Finnish point counts for landbirds which started in 1984. One point-count route includes 20 points, each of which are located in uniform habitats (within a 50-m radius) and separated by 250 m in forests and 350 m in open areas (Koskimies & Väisänen 1991, Laaksonen & Lehikoinen 2013). Each point was surveyed for five minutes, and observed birds were classified as inside or outside a 50-m radius from the point (Koskimies & Väisänen 1991). Point-count routes were performed once a year and they were annually censused from 20th May to 20th June in southern Finland and from 30th May to 30th June in northern Finland (Koskimies & Väisänen 1991). While habitat data are also provided in point-count routes, its precision is lower compared with that gathered from line-transects (e.g., average tree height is not specified).

The counting methods described above do not reveal the absolute unbiased abundances of species, nor the exact boundaries between the habitats used by birds. Nevertheless, the selected data can be used to reliably describe spatial and temporal variation in the general distribution of birds around the country (Väisänen & Lehikoinen 2013) and in different environments (line-transect censuses only; Koskimies & Väisänen 1991). Habitat-specific differences in detectability might distort our measures of preferences, and changes in species detectability due to earlier phenology could cause spurious trends. A study carried out by Lehikoinen (2013) showed that only three of 73 Finnish breeding landbird species showed an annual trend in the proportion of main-belt observations in line-transect data from 1987 to 2010. This suggests that a temporal change in detectability is at most a minor problem. Two of our study species displayed trends in the proportion of main-belt observations: Goldcrest (*Regulus regulus*) a positive trend, and Eurasian Jay (*Garrulus glandarius*) a negative one. However, both species were retained because such uniform trends in detectability did not explain true population change in either species, which increased at the beginning and declined at the end of the study period.

We included only line transects and point counts repeated at least twice during the study period. From 1984 until 2013 this resulted in an annual average of 94 line transects (range 38–184) and 47 point-count routes (range 26–86) in our study area (Laaksonen & Lehikoinen 2013, Lehikoinen *et al.* 2013b; Fig. 1). On a national scale, there was no temporal trend in the annual average latitudinal position or annual average census date of the transect lines during the study period (Lehikoinen 2013). Point counts comprised only 22% of the data. Annual statistics of the point-count routes can be viewed at the web page of the Finnish Museum of Natural History at https://rengastus.helsinki.fi/tuloksia/Pistelaskenta.

We used weather data, obtained from the Finnish Meteorological Institute, to describe the extent of temperature increase over the last decades during the breeding season (March–July) and the wintering season (December–February). We estimated the average temperatures for these two periods (based on daily means) to see whether fluctuations in the community latitude index (CLI; see section 2.5.) could be explained by weather. In addition, we built a model where we included temperatures for both the breeding and wintering seasons (see section 2.5.). Data were available from years 1984–2013, covering the study area with a 10 × 10 km grid.

## 2.2. Species selection and estimation of trends

To ensure the representativeness of species in forest habitats, we first assessed the preference for forest habitats over non-forest habitats based on line-transect habitat data. This was done by dividing the species' total densities (pairs / km) in forest habitat types (categories *a*–*g* according to the above classification) with the densities in non-forest habitat types (categories *h*–*l*). We selected only species whose densities in forest habitat types were 1.5 times higher relative to non-forest habitat types (i.e., having a minimum forest preference ratio of 1.5). In addition, the selected species were required to have at least 20 observations from the main belt to be able to estimate their habitat preferences. On this basis, a total of 32 common forest bird species from southern Finland were chosen for this study (see Appendix 1).

For all 32 species we separately calculated estimates and standard errors (SEs) for: i) piecewise log-linear temporal trends (log-growth rates) with a break-point at 1998.5 (period 1: 1984–1998; period 2: 1999–2013); and ii) annual indices for relative population density (always starting from 1 = abundance of summer 1984). Piecewise analysis offers more complex patterns of dynamics to be potentially explained rather than compared to a uniform trend. We wanted to use a common break-point for all species to make easily interpretable comparisons between them. Setting the break-point at 1998.5 makes the two time periods equally long and the trend estimates better comparable. In order to fit trends and annual population indices, we used the software package TRIM (TRends and Indices for Monitoring data; Pannekoek & van Strien 2005) version 3.53, which fits log-linear Poisson-models. Although not all the routes have been censused every year, TRIM handles such missing data through imputation. Both over-dispersion and temporal autocorrelation were accounted for using a quasi-Poisson approach and generalized estimation equations, respectively (Pannekoek & van Strien 2005).

## 2.3. Explanatory variables in the model

To determine the habitat-related variables for each species, we first averaged the route-specific observed number of pairs and surveyed km over the period 1986–2013, separately for the different habitat types. We used the same categories as mentioned in section 2.1. except for mountain areas (category *k*), which do not occur in the study area. We further calculated the species' densities (pairs / km of habitat) for the seven different forest habitat types (categories *a*–*g*), and average tree height was also estimated for each species and land-use category. Lastly, we computed three variables describing different habitat preferences for the study species (*LSH*, *NPH* and *Th*; see explanation below) and one variable related to the flexibility in habitat use (*Hab_ev*; see explanation below).

*LSH*: variable explaining the species' preference for a late successional habitat. It was calculated as the log-ratio of total densities in late successional habitats (i.e., spruce, pine, mixed and broadleaf forests, and pine mires) to early successional habitats (i.e., clear-cuts and bushes). As Greenish Warbler (*Phylloscopus trochiloides*) was absent in early successional habitats, we added the smallest observed non-zero density (0.0196) to all early successional habitat densities before the calculations were made.

Table 1. Correlation coefficients between the explanatory variables (the design matrix) in the trend pattern analysis. Migratory strategies are abbreviated as follows: *Partial* (partial migrants), *Short* (short-distance migrants), and *Long* (long-distance migrants). For the rest of the variables, the same nomenclature is used throughout the manuscript (see Material and Methods section). Residents are defined as the intercept in the model and therefore they are not included as another explanatory variable in the design matrix. Pairs of variables with strong correlations (abs(*r*) > 0.5; bolded) were not included in the same model simultaneously.

| | *LSH* | *NPH* | *Th* | *Hab_ev* | *Lat* | *Partial* | *Short* |
|---|---|---|---|---|---|---|---|
| *NPH* | –0.477 | – | – | – | – | – | – |
| *Th* | **0.742** | **–0.624** | – | | – | – | – |
| *Hab_ev* | **0.747** | **–0.512** | 0.480 | – | – | – | – |
| *Lat* | –0.300 | **0.595** | **–0.550** | –0.226 | – | – | – |
| *Partial* | –0.278 | 0.054 | –0.148 | –0.187 | 0.347 | – | – |
| *Short* | 0.203 | –0.248 | 0.385 | 0.079 | –0.196 | –0.249 | – |
| *Long* | 0.024 | 0.090 | –0.376 | 0.212 | 0.178 | –0.186 | –0.447 |

*NPH*: variable explaining the preference for nutrient-poor habitats (i.e., species favouring pine forests). It was calculated as the log-ratio of total densities in pine-dominated habitats (nutrient-poor environments) to total densities in spruce, mixed and broadleaf forests (nutrient-rich environments).

Mean tree height (*Th*): average tree height where the species had been observed in habitat types *a*–*g*.

Habitat evenness (*Hab_ev*): variable describing how specialist or generalist the species are in their habitat preferences (low values indicate habitat generalism). This was calculated using the following equation (Eq. 1):

$$Hab\_ev = \ln\left[6 \times \max(\mathbf{d}) / (\Sigma\mathbf{d} - \max(\mathbf{d}))\right] \qquad (1)$$

where **d** is a vector containing species' densities for the different forest habitat types ($n = 7$; categories *a*–*g*). All the species-specific values of the variables are given in Appendix 1.

Further, we used the variable "latitude" (*Lat*) which describes the average latitudinal distribution of each species in Finland in five different decades from the 1970s until 2012, as defined in Virkkala and Lehikoinen (2014). It was calculated by dividing the country in 50-km blocks according to latitude and estimating the block average densities (pairs / km) for each species using decadal breeding bird counts from the 1970s to 2012. Finally, "latitude" was established as the weighted average latitude (mid-points of each block), using block-specific densities as weights, and it was scaled so that one unit equalled 500 km. We did not recalculate the values exclusively for our study period because the magnitude of change in the latitudinal distribution during the 1970s to the 1980s was not significant (see Virkkala & Lehikoinen 2014).

Lastly, we classified the study species according to their migration strategy (hereafter *Migr*) into four factor levels: i) residents; ii) regular partial migrants (some individuals migrate and some do not); iii) regular short-distance migrants (most of the population is migratory); and iv) regular long-distance migrants (Laaksonen & Lehikoinen 2013). The majority of the study species were passerines (75%), the most frequently represented families being *Fringillidae* and *Sylviidae* (Appendix 1).

### 2.4. Statistical analyses

In order to assess the patterns of temporal trends for the study species, we applied multivariate regression, with a bivariate response matrix **Y** constructed from the species' trends of the two periods ($y_1$: 1984–1998 and $y_2$: 1999–2013). The first response variable (first column of **Y**) was the average trend of the two periods ($(y_1 + y_2) / 2$) and the second one was the change in the direction of the trends ($y_2 – y_1$). For multivariate regression we used "lm" in R version 3.0.2 (R Development Core Team 2013).

Table 2. The twenty competing models, the number of explanatory variables ($k$), the difference in CAIC compared to the most parsimonious model ($\Delta_i$), and CAIC weights ($w_i$). The two first listed models can be considered as the most parsimonious ones, and are given closer attention when interpreting the results.

| Model | $k$ | CAIC | $\Delta_i$ | $w_i$ |
|---|---|---|---|---|
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{LSH}\,\beta_1 + \mathit{NPH}\,\beta_2$ | 3 | –410.25 | 0.00 | 0.597 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{LSH}\,\beta_1 + \mathit{Lat}\,\beta_5$ | 3 | –408.53 | 1.71 | 0.253 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{LSH}\,\beta_1$ | 2 | –405.71 | 4.54 | 0.062 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0$ | 1 | –405.03 | 5.22 | 0.044 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Lat}\,\beta_5$ | 2 | –403.65 | 6.60 | 0.022 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{NPH}\,\beta_2$ | 2 | –401.91 | 8.34 | 0.009 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Hab\_ev}\,\beta_4$ | 2 | –400.43 | 9.82 | 0.004 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Th}\,\beta_3$ | 2 | –400.04 | 10.21 | 0.004 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Hab\_ev}\,\beta_4 + \mathit{Lat}\,\beta_5$ | 3 | –399.68 | 10.56 | 0.003 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{LSH}\,\beta_1 + \mathit{NPH}\,\beta_2 + \mathbf{M}\,\beta_6$ | 6 | –396.46 | 13.79 | 0.001 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{LSH}\,\beta_1 + \mathit{Lat}\,\beta_5 + \mathbf{M}\,\beta_6$ | 6 | –395.95 | 14.29 | 0.001 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathbf{M}\,\beta_6$ | 4 | –395.28 | 14.97 | 0.000 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Th}\,\beta_3 + \mathit{Hab\_ev}\,\beta_4$ | 3 | –395.15 | 15.10 | 0.000 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{LSH}\,\beta_1 + \mathbf{M}\,\beta_6$ | 5 | –394.42 | 15.83 | 0.000 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Lat}\,\beta_5 + \mathbf{M}\,\beta_6$ | 5 | –392.73 | 17.52 | 0.000 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{NPH}\,\beta_2 + \mathbf{M}\,\beta_6$ | 5 | –391.42 | 18.83 | 0.000 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Hab\_ev}\,\beta_4 + \mathbf{M}\,\beta_6$ | 5 | –389.46 | 20.78 | 0.000 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Th}\,\beta_3 + \mathbf{M}\,\beta_6$ | 5 | –389.41 | 20.84 | 0.000 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Hab\_ev}\,\beta_4 + \mathit{Lat}\,\beta_5 + \mathbf{M}\,\beta_6$ | 6 | –387.46 | 22.78 | 0.000 |
| $\mathbf{Y} \sim \mathrm{I}\,\beta_0 + \mathit{Th}\,\beta_3 + \mathit{Hab\_ev}\,\beta_4 + \mathbf{M}\,\beta_6$ | 6 | –382.56 | 27.68 | 0.000 |

To evaluate which subset of six explanatory variables best described the multivariate pattern of our trends, we used information theoretical model selection (Burnham & Anderson 2002). The four-level factor "migration strategy" (*Migr*), as well as five continuous variables (*LSH*, *NPH*, *Th*, *Hab_ev* and *Lat*) all centered to 0 mean, were used to construct the competing candidate models. The full model with all variables included can be written as follows:

$$\mathbf{Y} = \mathrm{I}\,\beta_0 + \mathit{LSH}\,\beta_1 + \mathit{NPH}\,\beta_2 + \mathit{Th}\,\beta_3 + \mathit{Hab\_ev}\,\beta_4 + \mathit{Lat}\,\beta_5 + \mathbf{M}\,\beta_6 + \varepsilon, \tag{2}$$

where I is an $n$-by-1 column vector of ones, $\beta_0$ and $\beta_1$–$\beta_5$ are two element row vectors with intercept terms and regression coefficients, respectively, $\mathbf{M}$ is an $n$-by-3 matrix of dummy variables coding for migratory strategy, $\beta_6$ is a corresponding 3-by-2 matrix with level specific average differences compared with residents, and $\varepsilon$ is an $n$-by-2 matrix or bivariate normally distributed error terms.

The competing models considered were all possible subsets of explanatory variables whose maximum Pearson's correlation coefficient was below 0.5 (see correlation matrix in Table 1). This was done to avoid problems of collinearity, and is according to the most restrictive suggestion for threshold found in Booth *et al*. (1994). We finally obtained a total of 20 different models (see Table 2).

The selected models were evaluated according to their parsimony, based on their CAIC values (Consistent Akaike's Information Criterion; Burnham & Anderson 2002), and they were calculated separately from the bivariate model residuals employing the formula proposed by Fujikoshi and Satoh (1997); see Eq. 3–4. CAIC is intended for fully parameterized multivariate regression models for $n$ independent multivariate observations, assuming multinormally distributed residuals.

$$\mathrm{CAIC} = \mathrm{AIC} + 2K \times (k + 1 + p) \,/\, (n - k - 1 - p) \tag{3}$$

$$\mathrm{AIC} = n \times \ln(\det(\mathbf{C})) + 2K \tag{4}$$

where $K$ is the total number of estimated parameters, $k$ the no. of explanatory variables (including the intercept), $p$ the no. of response variables, and $\det(\mathbf{C})$ is the determinant of the residual covariance matrix (residual sum of squares and cross products matrix – SSCP – divided by $n$).

Table 3. Estimated effect sizes (Estimate), standard errors (SE), and annual multiplicative changes in percentages (% Change) of variables explaining the patterns in logarithmic temporal trends of breeding forest birds. Results are shown for the two most parsimonious models, the better one being listed first. The two response variables in the models were the average trends for periods 1 ($y_1$: 1984–1998) and 2 ($y_2$: 1999–2013), and the change in the trend at the break-point (1998.5). The estimated residual standard deviation (Residual SD) is also presented in the table. Coefficients differing significantly from zero are bolded.

| | Average trend: $(y_1 + y_2) / 2$ | | | Change in trends: $y_2 - y_1$ | | |
|---|---|---|---|---|---|---|
| Variable | Estimate | SE | % Change | Estimate | SE | % Change |
| Model: $\mathbf{Y} \sim I\,\beta_0 + LSH\,\beta_1 + NPH\,\beta_2$ | | | | | | |
| Intercept | –0.0005 | 0.0038 | –0.1 | **–0.0257** | **0.0107** | **–2.5** |
| *LSH* | **–0.0295** | **0.0076** | **–2.9** | 0.0063 | 0.0215 | 0.6 |
| *NPH* | **–0.0182** | **0.0060** | **–1.8** | 0.0137 | 0.0170 | 1.4 |
| Residual SD | 0.0214 | – | – | 0.0606 | – | – |
| Model: $\mathbf{Y} \sim I\,\beta_0 + LSH\,\beta_1 + Lat\,\beta_5$ | | | | | | |
| Intercept | –0.0005 | 0.0040 | –0.1 | **–0.0257** | **0.0104** | **–2.5** |
| *LSH* | **–0.0238** | **0.0073** | **–2.4** | –0.0105 | 0.0193 | –1.0 |
| *Lat* | **–0.0304** | **0.0124** | **–3.0** | –0.0485 | 0.0327 | –4.7 |
| Residual SD | 0.0224 | – | – | 0.0590 | – | – |

## 2.5. Forest breeding bird indices

For future monitoring purposes, we constructed three different multi-species indices (cf., "indicators"; Gregory *et al*. 2005), all intended to summarize the state of the forest bird community in southern Finland, and patterns from trend analysis. Two of the indices were related to the species habitat preferences, and one was related to their latitudinal distribution.

For the first one, called the late successional habitat index (hereafter LSH-index), annual estimates of relative abundance obtained from TRIM were used to calculate a weighted geometric mean, where each species' abundance was weighted by the *LSH* variable (see section 2.3.; Gregory *et al.* 2005). Therefore, the LSH-index reflects the positive or negative contribution of the species living in late and early successional forest habitats, respectively. In order to understand which part of the bird assemblage was driving the trend, we produced a second, similar mature forest index (hereafter MF-index) only including species with a clear preference for old stands. This was also done to check for consistency between the two approaches, acknowledging that the MF-index is easier to calculate and closer to the indices familiar to many practitioners. The species selection was based on the ratio of total densities in late and early successional habitats (see Appendix 1). Species with at least two times higher densities in late successional habitats than in early successional habitats (or alternatively $LSH \geq 0.693$) were included in this index ($n = 13$; see Appendix 1). We analysed the temporal variation of the LSH- and MF-indices using piecewise linear regression (package segmented; Muggeo 2003, 2008) and ordinary linear regression with year as explanatory variable. In the piecewise linear model, we allowed for a possible change in the trend with an estimated break-point for year (two additional parameters estimated). We used likelihood ratio tests to compare this approach with the null model, where the trend was constant throughout the period. The null models were applied whenever the tests were statistically non-significant.

We also built a community latitude index (hereafter CLI) illustrating the relative representation of southern and northern species. To do this, we used the earlier mentioned species-specific mean "latitude" values from 1970–2012 and calculated the weighted arithmetic mean latitude of the community for each year (1984–2013) using the species-specific abundance indices as weights.

A negative temporal trend in the community latitude index would imply that southern species have become more common, and *vice versa*. Finally, we also analysed the temporal variation of CLI using piecewise and ordinary linear regression models. Again, we allowed for a possible change in the trend with an estimated break-point for year in the piecewise linear model. Likelihood ratio tests were also used to compare this approach with the null model, with a constant trend throughout the period. As next step, we added the average temperatures for both the breeding and wintering seasons as explanatory variables to the chosen trend model (see section 2.1.). The correlation between breeding and wintering temperatures was low ($r$ = 0.13).

## 3. Results

The results from the information-theoretic approach revealed that there were two models supported over the others in terms of parsimony (CAIC weights of two best models: $w_i = 0.597$ and $w_i = 0.253$; difference in CAIC between best and third best model $\Delta_i = 4.54$; Table 2). The average trend for all species included was close to zero (–0.1%) and non-significant (Table 3). Importantly, in both models the change in population trends was on average –3% after the break-point, i.e., the average decline has become steeper (Table 3; the intercept of $y_2 - y_1$). This implies an average increase in the first period, followed by a decline in the second one. The between-species variation in the observed change in trends was not explained by any of the predictors (Table 3).

Both best models included the preference for late successional habitats (*LSH*) as an explanatory variable, which was negatively related to the average trend observed (in the best model: $b = -0.030 \pm 0.008$ SE, $t = 3.87$, $df = 29$, $p < 0.001$; Table 3, Fig. 2A). This implies that species with exp[1] = ca 2.72 times higher densities in late successional habitats relative to densities in early successional habitats showed on average ca –3% additional annual change in population density. In the second best model, the negative effect of *LSH* on the population trends was slightly smaller (–2.4%; $b = -0.024 \pm 0.007$ SE, $t = 3.26$, $df = 29$, $p = 0.003$; Table 3).

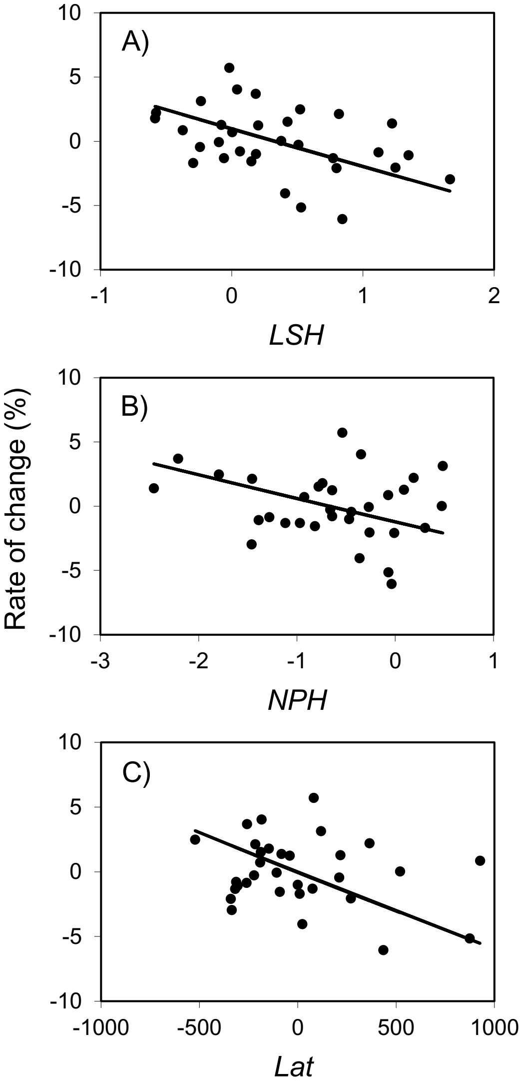

Fig. 2. Average population trends (expressed as percentages of growth) of the study species in relation to A) the preference for late successional habitats (*LSH*), B) the preference for nutrient-poor habitats (*NPH*), and C) latitudinal distribution (*Lat*). The black solid lines represent the partial effects of *LSH* (estimated for the most parsimonious model; Table 3), *NPH* and *Lat* (centered to zero mean), respectively.

In addition to *LSH*, the best model had a negative effect of nutrient-poor habitats on the average trend (*NPH*: $b = -0.018 \pm 0.006$ SE, $t = 3.03$, $df = 29$, $p = 0.005$), i.e., species preferring nutrient-poor habitats (ca 2.72 higher densities compared to nutrient-rich habitats) had a –1.8% additional an-

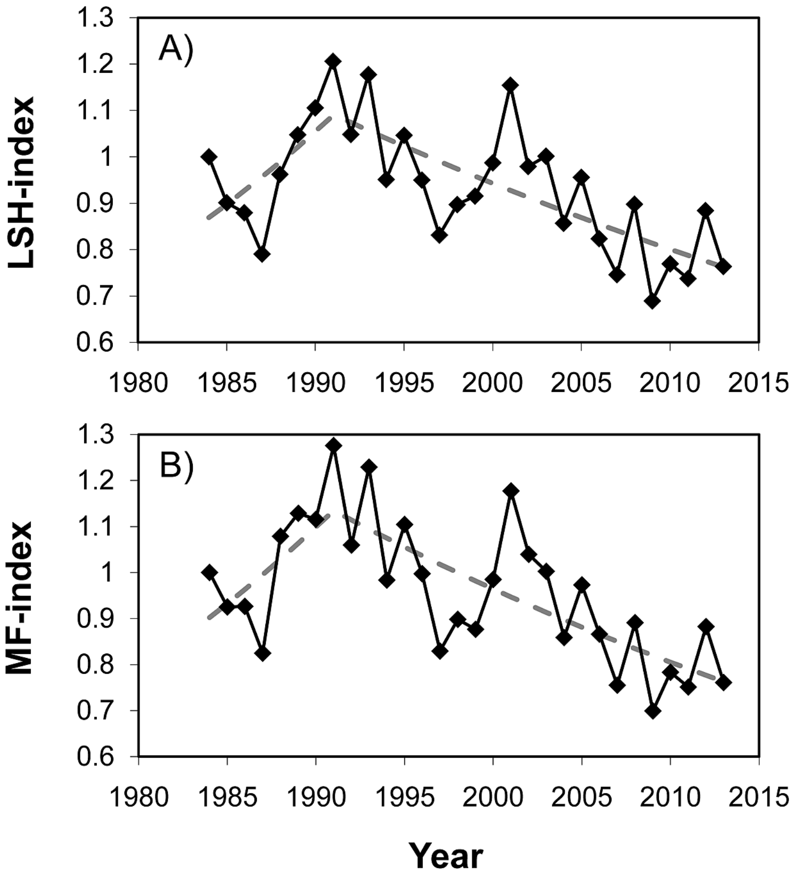

Fig. 3. A) LSH-index reflecting the positive or negative contribution of the species living in late and early successional forest habitats; B) MF-index of 13 forest species preferring late stages of succession. These indices are based on the (weighted) geometric means of annual species-specific abundances in 1984–2013. Annual indices for relative population density always start from 1 (in 1984; see appendix A in Gregory *et al.* 2005). The dashed grey lines in both panels represent segmented regressions against year.

nual change in population density (Table 3, Fig. 2B). In the second best model, latitudinal distribution – instead of *NPH* – had a negative effect on the average trend (*Lat*: $b = -0.030 \pm 0.012$ SE, $t = 2.45$, $df = 29$, $p = 0.020$). This implies that southern species populations were increasing relative to northern species populations, and that annual population trends changed on average –3% / 500 km latitude (Table 3, Fig. 2C).

The third variable related to forest preferences (*Th*) did not explain the species-specific population trends for any of the response variables. Neither flexibility in habitat use (defined as *Hab_ev*) nor migratory strategy had any effect on the trends (Table 2).

Among the 32 study species, 12 showed significant positive population trends and nine negative trends in the first period (1984–1998), whereas only six species were significantly increasing and 15 significantly decreasing during the second period (1999–2013). The remaining 11 species, from 1984–1998 and from 1999–2013, respectively, showed no significant trends (Appendix 1).

The four most rapidly increasing species that have more than doubled throughout the whole study period (1984–2013) were Red Crossbill (*Loxia curvirostra*; population growth +401%), Black Woodpecker (*Dryocopus martius*; +215%), Eurasian Wren (*Troglodytes troglodytes*; +186%) and Mistle Thrush (*Turdus viscivorus*; +145%). Red Crossbill increased in both periods, but showed a more rapid increase in the second period. The other three species increased much more in the first period, and Eurasian Wren even showed a statistically significant moderate decline in the second period.

The four most declining species, which have declined to less than half over the whole study period, were Rustic Bunting (*Emberiza rustica*; –84%), Brambling (*Fringilla montifringilla*; –78%), Willow Tit (*Parus montanus*; –70%) and Wood Warbler (*Phylloscopus sibilatrix*; –58%).

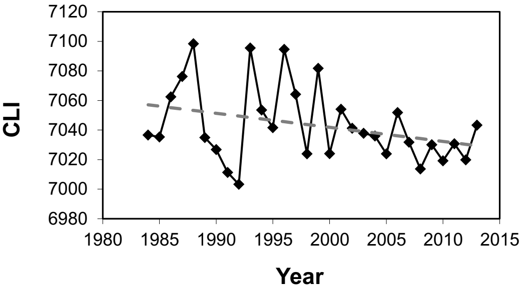

Fig. 4. Time series of the community latitude index (CLI) during the period 1984–2013 summarizing the representation of species with southern and northern breeding distributions. The index is calculated from the weighted average latitude of species (see section 2.3. and section 2.5.), where weights are the relative abundance indices for the 32 study species. The dashed grey line are fitted values of the linear regression against year. Notice that one unit of CLI equals 1 km.

All these species showed significant negative trends in both periods, and with the exception of Wood Warbler, all showed clearly stronger declines in the second period.

Other species with significant and noteworthy trends in both periods were, e.g., Eurasian Bullfinch (*Pyrrhula pyrrhula*), Common Redpoll (*Carduelis flammea*), Goldcrest (*Regulus regulus*) and Eurasian Jay (*Garrulus glandarius*), all showing an increase in the first period and a decrease in the second period. In addition, Common Chiffchaff (*Phylloscopus collybita*) showed the opposite pattern, with a strong decline in the first period and a clear increase in the second period. For all but Common Redpoll the net change for the whole period was negative (Appendix 1).

The LSH-index illustrates the general decline of species preferring late successional stages (Piecewise linear regression, $b_1 = 0.033 \pm 0.020$ SE, $b_2 = -0.016 \pm 0.003$ SE; Likelihood ratio test, $\chi^2 = 12.05$, $df = 2$, $p = 0.002$; Fig. 3A). We identified the approximate year where the decline started by allowing the model to determine the break-point through a numerical search. Therefore, the MF-index showed a decrease of ~40% since the beginning of 1991 (Piecewise linear regression, $b_1 = 0.033 \pm 0.020$ SE, $b_2 = -0.018 \pm 0.003$ SE; Likelihood ratio test, $\chi^2 = 12.18$, $df = 2$, $p = 0.002$; Fig. 3B). The indices LSH and MF had a very strong positive correlation ($r = 0.98$).

For CLI, a piecewise linear trend with an estimated break-point was not significantly better compared to a linear trend (Likelihood ratio test, $\chi^2 = 1.81$, $df = 2$, $p = 0.404$). The mean latitude of the bird community was shifting almost significantly ~30 km southwards in the last 30 years (Linear regression, $b = -0.953$ km / year ± 0.517 SE, $F_{1,28} = 3.40$, $p = 0.076$; Fig. 4). Importantly, CLI was associated with breeding temperature when both temperature variables were added as covariates to the model with a linear trend (Multiple regression, breeding temperature: $b = -10.912$ km / °C ± 5.006 SE, $t = 2.18$, $df = 26$, $p = 0.039$; winter temperature: $b = -1.395$ km / °C ± 1.416 SE, $t = 0.99$, $df = 26$, $p = 0.334$). The temperatures themselves did not show a significant increase during the study period (Linear regression, breeding temperature: $b = 0.023$°C / year ± 0.018 SE, $F_{1,28} = 1.60$, $p = 0.217$; winter temperature: $b = 0.075$°C / year ± 0.064 SE, $F_{1,28} = 1.36$, $p = 0.253$).

## 4. Discussion

The average pattern of trends indicated no long-term change in all species included, but a slight increase during the first 15 years, followed by a decrease (ca –3% change) in the last 15 years. Species-specific variation in the change of trend direction could not be explained by any of the predictor variables included in our study. Hence, all the species-specific differences explained by the models concerned long-term trends.

In Finland, habitat loss and fragmentation have been considered as the two principal causes of population decline in old-growth forest bird species since the 1950s (Järvinen *et al.* 1977, Helle & Järvinen 1986, Väisänen *et al.* 1998, Virkkala 1987, Fraixedas *et al.* 2015), especially due to changes in the forest age structure (Rauhala 1983, Väisänen 1983, Virkkala *et al.* 1993). Our main findings confirm an increased loss of birds preferring mature forests in southern Finland. The community-level LSH- and MF-indices both capture the general pattern of decline and an acceleration since approximately 1991.

Importantly, habitat preferences were significant in explaining bird population trends. Species preferring late successional habitats had more negative population trends than species preferring early successional stages. Given both the decline in the proportion of mature forests and the increase in the proportion of young age classes, which has been going on for decades in Finland (Parviainen & Västilä 2012), changes in forest structure probably explain the general decrease of mature forest bird species. In contrast, the increasing populations of species preferring early successional stages in Finland was already noted in the 1970s (Järvinen *et al.* 1977) and has been mostly attributed to the large-scale clear-cuts that took place after the Second World War (Miettinen *et al.* 2008, Kovalainen & Seppo 2009). Our results also indicated that populations of species preferring nutrient-poor, primarily northern coniferous, habitats had more negative trends relative to species associated with nutrient-rich, primarily southern, deciduous habitats (see Merilä *et al*. 2014). This may be aggravated by climate change, which is predicted to increase the proportion of deciduous forests in South Finland (Parviainen & Västilä 2012), and is contributing to northward shifts in associated species distributions and densities (e.g., Virkkala & Lehikoinen 2014).

Several earlier studies have documented that species distributions and abundances of various taxa are moving polewards, probably due to climate change (Parmesan 2006, Jiguet *et al.* 2010b, Chen et al. 2011). This is also the case for birds in Finland (Virkkala & Rajasärkkä 2011, 2012, Brommer *et al.* 2012, Virkkala & Lehikoinen 2014). In addition, northern species have declined compared to southern species (Laaksonen & Lehikoinen 2013). In the present study, our community latitude index (CLI) was not able to clearly capture the effect of latitude found in the multivariate analysis. However, it showed a tendency for a trend in the southern latitudes, which means increased representation of southern species in the entire breeding forest community and thus a general shift of the bird community towards the north. The change in CLI (~1.0 km / year) was very similar to what has been found in previous Finnish studies of distribution (0.7–1.3 km / year) and density shifts (1.3 km / year) (Virkkala & Lehikoinen 2014). The fact that species may be expanding or retracting their ranges as a consequence of the rise in global temperatures (Brommer *et al*. 2012, Virkkala & Lehikoinen 2014) suggests that this pattern may become more pronounced during the next decades. Climate change is expected to have a greater effect on northern latitudes, making these regions especially vulnerable (Pachauri & Reisinger 2007). The temperature increase in Finland has nearly doubled compared to the global temperature increase in the last 166 years (Mikkonen *et al*. 2014), and temperatures in southern Finland have significantly increased by 1.4°C since the 1970s (Virkkala & Lehikoinen 2014). Although temperature for the breeding season did not show any trend during the study period, it had a significant negative effect on CLI, meaning that temperature may partly explain the fact that southern species are increasing their representation in the whole bird community.

Variables such as migratory strategy (*Migr*), habitat evenness (*Hab_ev*) and tree height preference (*Th*) had no significant correlative effects on population trends in this study. However, some of them have proved to be relevant correlates of patterns in population trends in other studies, none of which concern exclusively forest birds. Migration strategy has explained variation in bird population trends in Finland both during the breeding and wintering seasons (e.g., Virkkala *et al.* 2013, Laaksonen & Lehikoinen 2013, Fraixedas *et al.* 2015). Nevertheless, the reason why we did not detect effects, such as the general decline of long-distance migrants (Vickery *et al.* 2014), could be because our study was concentrating on patterns in one particular habitat type, where other factors such climate or land-use change may be currently more important (Hewson & Noble 2009). The lack of any effect of flexibility in species' habitat use (captured by the variable *Hab_ev*) may be due to the nature of our study species. All of them are common forest breeders, which surely can occur in different forest typer. Still the rare and more extreme habitat specialists might encounter problems Although several studies have shown that old-growth forest specialists are strongly negatively affected by forest management (Helle 1985, Väisänen *et al*. 1986, Virkkala 1991), there seems to be complex effects on the resources needs of common slightly more adaptable species.

In conclusion, the general long-term decline of mature forest birds in our study area has escalated in recent years. Species that deserve special attention are Rustic Bunting, Brambling, Willow Tit and Wood Warbler, which consistently declined throughout the period. The observed patterns may be likely, at least partly, linked with both forest management and climate change. Some of the summarizing indices presented here (at least LSH and MF) may help to monitor the effect of these factors in the future. Given that current conservation programmes have shown no signs of stopping the population decline of Finland's mature forest birds, additional conservation resources are needed for the future preservation of the avifauna in boreal forests in southern Finland. Importantly, the impact of the conservation actions should be evaluated on a regular basis.

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### Metsälintujen pesimäkantojen muutokset Etelä-Suomessa

Metsätalous on johtanut luontaisten metsien ja niissä elävien lajien kantojen vähenemiseen Suomessa. Eteläisessä Suomessa vain prosentti metsäpinta-alasta on suojeltu, mutta silti metsätalouden vaikutukset yleisiin metsälintulajeihin on tunnettu puutteellisesti. Tässä työssä selvitimme, miten 32 metsälintulajin kannankehitykset Etelä-Suomessa olivat yhteydessä lajikohtaiseen habitaatinvalintaan, muuttokäyttäytymiseen ja levinneisyyteen. Tarkastelimme kannanmuutoksia kahdessa eri jaksossa (1984–1998 ja 1999–2013) hyödyntäen linja- ja pistelaskennoilla kerättyä seuranta-aineistoa. Linjalaskentojen pääsarkahavaintojen perusteella pystyimme laskemaan minkälaista habitaattia (kuusi-, mänty-, seka- ja lehtimetsät; hakkuuaukeat, pensaikot ja puustoiset rämeet) ja puustonkorkeutta lajit suosivat.

Yleisten metsälajien kannankehitykset olivat keskimäärin negatiivisempia jälkimmäisellä tutkimusjaksolla, eli väheneminen on ollut kiihtyvää. Sukkession loppuvaiheiden elinympäristöjä (varsinaisia metsiä) suosivilla lajeilla väheneminen on ollut voimakkaampaa kuin pensaikkoja ja hakkuuaukeita suosivilla lajeilla. Lisäksi karuja elinympäristöjä (mäntymetsiä ja rämeitä) suosivat lajit, eli pääsääntöisesti pohjoiset lajit, taantuivat verrattuna rehevissä elinympäristöissä viihtyviin eteläisiin lajeihin.

Tulosten perusteella kehitimme kolme indeksiä, joita voidaan käyttää metsälinnuston yleisten muutosten seurannassa. Tuloksemme viittaavat siihen, että Suomessa yleisten metsälintujen kannanmuutoksiin ovat vaikuttaneet vanhojen metsien väheneminen sekä ilmastonmuutos, joka siirtää lajien levinneisyysalueita kohti pohjoista. Metsälintujen taantumisen pysäyttämiseksi, tulisi eteläisen Suomen metsien suojelua tehostaa.

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**Appendix 1.** The 32 study species, average annual sample sizes, estimated population trends (± SE) for periods 1 (1984–1998) and 2 (1999–2013), percentages of multiplicative net change, ratio of total densities in late and early successional habitats, and the six explanatory variables in the model: *LSH*, *NPH*, *Th*, *Hab_ev*, *Lat*, and *Migr* (the main migration strategies; r = resident, p = partial migrant, s = short-distance migrant and l = long-distance migrant). The ratios are bolded for species with at least two times higher densities in late successional habitats than in early successional habitats (or alternatively *LSH* ≥ 0.693; also bolded). As Greenish Warbler was not present in early successional stages, the ratio is not defined. Nevertheless, this species was regarded to prefer late successional stages (see *LSH* value).

| Common and scientific name of species | Avg. sample size | Trends ± SE | |
|---|---|---|---|
| | | Period 1 | Period 2 |
| Hazel Grouse (*Tetrastes bonasia*) | 50 (17–129) | –0.0234 ± 0.0130 | –0.0079 ± 0.0122 |
| Western Capercaillie (*Tetrao urogallus*) | 16 (5–49) | 0.0120 ± 0.0279 | **–0.0533 ± 0.0236** |
| Eurasian Woodcock (*Scolopax rusticola*) | 27 (11–59) | 0.0106 ± 0.0180 | 0.0316 ± 0.0159 |
| Common Greenshank (*Tringa nebularia*) | 46 (18–120) | 0.0289 ± 0.0159 | **–0.0284 ± 0.0141** |
| Green Sandpiper (*Tringa ochropus*) | 136 (54–350) | **0.0343 ± 0.0087** | 0.0013 ± 0.0068 |
| Common Cuckoo (*Cuculus canorus*) | 550 (238–1,225) | **–0.0119 ± 0.0052** | **0.0374 ± 0.0045** |
| Black Woodpecker (*Dryocopus martius*) | 62 (23–161) | **0.0663 ± 0.0135** | 0.0129 ± 0.0102 |
| Great Spotted Woodpecker (*Dendrocopos major*) | 238 (53–618) | **–0.0253 ± 0.0073** | **0.0241 ± 0.0057** |
| Tree Pipit (*Anthus trivialis*) | 1,336 (609–2,445) | **–0.0290 ± 0.0030** | –0.0051 ± 0.0027 |
| Eurasian Wren (*Troglodytes troglodytes*) | 83 (10–226) | **0.1019 ± 0.0128** | **–0.0294 ± 0.0083** |
| Hedge Accentor (*Prunella modularis*) | 309 (341–690) | **0.0122 ± 0.0061** | 0.0021 ± 0.0051 |
| European Robin (*Erithacus rubecula*) | 887 (368–2,366) | **0.0254 ± 0.0044** | 0.0049 ± 0.0035 |
| Song Thrush (*Turdus philomelos*) | 845 (396–2,052) | –0.0036 ± 0.0036 | **0.0283 ± 0.0035** |
| Mistle Thrush (*Turdus viscivorus*) | 65 (20–204) | **0.0453 ± 0.0170** | 0.0165 ± 0.0117 |
| Greenish Warbler (*Phylloscopus trochiloides*) | 13 (1–70) | 0.0453 ± 0.0386 | –0.0177 ± 0.0260 |
| Wood Warbler (*Phylloscopus sibilatrix*) | 279 (110–541) | **–0.0345 ± 0.0054** | **–0.0256 ± 0.0066** |
| Common Chiffchaff (*Phylloscopus collybita*) | 243 (57–556) | **–0.0761 ± 0.0072** | **0.0497 ± 0.0061** |
| Willow Warbler (*Phylloscopus trochilus*) | 4,719 (2,616–7,633) | **0.0108 ± 0.0017** | **–0.0196 ± 0.0018** |
| Goldcrest (*Regulus regulus*) | 387 (198–821) | **0.0333 ± 0.0051** | **–0.0504 ± 0.0048** |
| Willow Tit (*Parus montanus*) | 237 (85–424) | **–0.0259 ± 0.0060** | **–0.0567 ± 0.0060** |
| Crested Tit (*Parus cristatus*) | 146 (60–321) | 0.0028 ± 0.0080 | **–0.0450 ± 0.0070** |
| Coal Tit (*Periparus ater*) | 52 (9–132) | 0.0344 ± 0.0174 | 0.0146 ± 0.0144 |
| Eurasian Treecreeper (*Certhia familiaris*) | 87 (32–200) | 0.0165 ± 0.0108 | **–0.0383 ± 0.0092** |
| Eurasian Jay (*Garrulus glandarius*) | 76 (40–122) | **0.0259 ± 0.0100** | **–0.0415 ± 0.0092** |
| Common Raven (*Corvus corax*) | 57 (18–149) | 0.0117 ± 0.0139 | **0.0321 ± 0.0128** |
| Eurasian Chaffinch (*Fringilla coelebs*) | 5,420 (2,771–11,446) | **–0.0052 ± 0.0016** | –0.0002 ± 0.0017 |
| Brambling (*Fringilla montifringilla*) | 113 (27–267) | **–0.0258 ± 0.0102** | **–0.0798 ± 0.0214** |
| Eurasian Siskin (*Carduelis spinus*) | 1,095 (469–2,261) | 0.0051 ± 0.0035 | **–0.0251 ± 0.0033** |
| Common Redpoll (*Carduelis flammea*) | 46 (2–148) | **0.0815 ± 0.0280** | **–0.0643 ± 0.0189** |
| Red Crossbill (*Loxia curvirostra*) | 187 (15–882) | **0.0334 ± 0.0153** | **0.0777 ± 0.0130** |
| Eurasian Bullfinch (*Pyrrhula pyrrhula*) | 134 (74–210) | **0.0663 ± 0.0074** | **–0.0926 ± 0.0071** |
| Rustic Bunting (*Emberiza rustica*) | 23 (4–54) | **–0.0465 ± 0.0166** | **–0.0784 ± 0.0299** |

| % Net change | Ratio | *LSH* | *NPH* | *Th* | *Hab_ev* | *Lat* | *Migr* |
|---|---|---|---|---|---|---|---|
| –36 | 1.49 | 0.350 | –0.816 | 12.689 | 0.637 | 13.984 | r |
| –45 | **8.52** | **1.449** | –0.262 | 15.460 | 0.950 | 14.344 | r |
| 84 | **3.32** | **1.017** | –1.456 | 14.457 | 1.985 | 13.856 | s |
| 1 | **2.14** | **0.578** | 0.472 | 12.659 | 1.448 | 14.592 | l |
| 68 | 0.69 | –0.385 | –0.742 | 11.668 | 0.456 | 13.928 | l |
| 45 | 1.14 | 0.120 | 0.087 | 12.305 | 0.253 | 14.288 | l |
| 215 | 1.35 | 0.242 | –0.349 | 13.638 | 0.766 | 13.892 | r |
| –2 | 1.12 | 0.102 | –0.270 | 13.443 | 0.750 | 13.968 | r |
| –39 | 0.91 | –0.093 | 0.303 | 12.016 | 0.201 | 14.084 | l |
| 186 | 1.52 | 0.384 | –2.208 | 15.457 | 0.792 | 13.816 | s |
| 23 | 1.24 | 0.204 | –0.925 | 13.031 | 0.531 | 13.880 | s |
| 55 | 1.88 | 0.626 | –0.780 | 13.654 | 0.614 | 13.884 | s |
| 43 | 1.50 | 0.402 | –0.642 | 14.178 | 0.601 | 14.032 | s |
| 145 | 1.00 | –0.035 | 0.484 | 13.341 | 0.618 | 14.192 | s |
| 49 | – | **1.423** | –2.456 | 15.158 | 1.986 | 13.992 | l |
| –58 | **6.91** | **1.863** | –1.461 | 16.392 | 1.653 | 13.736 | l |
| –32 | **2.73** | **0.973** | –1.119 | 15.095 | 1.142 | 13.756 | s |
| –12 | 0.96 | –0.042 | –0.446 | 11.834 | 0.749 | 14.284 | l |
| –22 | **3.80** | **1.319** | –1.282 | 16.550 | 1.644 | 13.812 | s |
| –70 | 1.86 | 0.606 | –0.362 | 14.028 | 0.439 | 14.096 | r |
| –46 | **2.81** | **0.998** | –0.010 | 14.848 | 0.855 | 13.732 | r |
| 104 | **2.24** | **0.721** | –1.795 | 15.863 | 0.957 | 13.552 | r |
| –27 | **5.17** | **1.548** | –1.390 | 18.110 | 1.303 | 13.768 | s |
| –20 | 1.35 | 0.264 | –0.642 | 13.659 | 0.597 | 13.760 | r |
| 89 | 0.72 | –0.377 | 0.188 | 12.704 | 0.656 | 14.440 | r |
| –8 | **2.03** | **0.709** | –0.661 | 14.624 | 0.589 | 13.852 | s |
| –78 | **2.26** | **0.729** | –0.070 | 14.119 | 0.597 | 14.948 | s |
| –25 | 1.47 | 0.385 | –0.469 | 13.875 | 0.502 | 14.072 | s |
| 28 | 0.88 | –0.174 | –0.072 | 11.449 | 0.254 | 15.000 | p |
| 401 | 1.22 | 0.181 | –0.538 | 14.092 | 0.638 | 14.156 | p |
| –32 | 1.18 | 0.141 | –0.970 | 14.066 | 0.864 | 14.148 | p |
| –84 | **3.79** | **1.044** | –0.038 | 11.171 | 1.542 | 14.508 | l |