RESEARCH PAPER

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Increasing numbers of wintering forest birds in Swedish Lapland 1986–2017 show stronger correlations with forest development than with local weather

Ökande antal övervintrande skogsfåglar i Lappland 1986–2017 visar starkare samband med skogens utveckling än lokalt väder

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AFTER A LONG period of decline, the number of forest birds has increased in Sweden in recent decades. Whether this trend is due to an increase in forested area, forest quality, climate change, or a combination of these factors, remains unclear. Here, we compared forest bird data from a local winter point count route around Storuman in Swedish Lapland between 1986 and 2017, with the development of regional forest composition and local weather conditions. We suggest that rather than changes in average annual, winter, or summer local temperatures or precipitation, the main drivers behind increasing numbers of wintering forest birds in this part of Sweden are an increase in the area of denser forest and dead wood volume, and a decrease in open ground area without forest vegetation. While there may be supplementary explanations behind the increasing numbers of forest birds, such as reduced agriculture, decreasing local human population, or stronger photosynthesis, our results indicate that local land use has been favourable for forest birds in recent decades in this area.

Introduction

Biodiversity loss is a possible threat to humanity's future (Cardinale *et al.* 2012). From 1970 to 2014, population sizes of mammals, birds, fish, reptiles, and amphibians around the globe declined by on average 60 % (WWF 2018). A global key question is how we can manage land use so that it contributes to the well-being of humans, without jeopardizing the rest of life on Earth.

In Sweden, even-aged silviculture has been the most common forestry practice since the middle of the 20th century (Lundmark *et al.* 2013). After debating the environmental effects of this practice for decades, the latest Swedish Forestry Act of 1993 stated that environmental and wood production targets should be equally important (Bush 2010). Stronger environmental targets led to the development of current certification standards, and about 60 % of Sweden's productive forest has been certified during the last 20–25 years (PEFC 2019, FSC 2019). These standards aim at improving conditions for biodiversity by, for example, saving groups of trees and dead wood, and creating high stumps during harvesting. However, several studies have shown that the levels of tree retention, volume of dead wood created etc. within today's certification systems are too low to maintain a more natural biodiversity within managed forests, although they do improve conditions compared to not taking these actions (Söderström 2009, Andersson *et al.* 2015, Odsen *et al.* 2018, Basile *et al.* 2019).

Birds are a good proxy for overall biodiversity, as they are easy to study, well-known, and high in the food chain. A rich birdlife is likely to reflect a rich biodiversity at a general level (Roberge & Angelstam 2006, Pakkala *et al.* 2014), and the number of breeding bird species in Sweden has increased continuously since 1850 (Haas *et al.* 2014). European bird distributions are expected to shift northwards and upwards in altitude due to the ongoing global warming (Barbet-Massin *et al.* 2012, Virkala & Lehikoinen 2017). Warming can affect bird community composition at local and national levels relatively rapidly (Devictor *et al.* 2008, Godet *et al.* 2011, Lindström *et al.* 2013, Lehikoinen *et al.* 2016, Lindström 2018).

While the number of breeding bird species in Sweden has increased at a slow but constant rate since 1850 (Haas *et al.* 2014), the abundance of forest birds has most likely been declining for a long period in Sweden (Green *et al.* 2019). However, during the last 20 years (1998–2018), general forest bird abundance has increased (Green *et al.* 2019). This development coincides with the implementation of the latest Swedish Forest Act from 1993. Nevertheless, it remains to be tested whether the positive development is due to increased forested area, forest quality, climate change, or a combination of these factors (Ram *et al.* 2017).

Here we analyse data for birds breeding in forest habitats, but the data is collected during winter time. Data are from a local winter point count route around Storuman in Swedish Lapland between 1986 and 2017, and we compare bird data with the development of regional forest composition and local weather conditions in an attempt to shed more light on this question.

Because most bird species that breed in Sweden spend a large part of the year in other parts of the world, it is best to analyse the effects of changes in Swedish land use and climate on birds that are resident in the country. The absolute majority of the forest bird species included in this analysis do spend the whole year in Sweden. Furthermore, most of them also spend the whole year within the same region, even though they probably use areas closer to human settlements in winter, hence making them easier to count. We also included a few (five out of 35) species that are mostly migratory. The majority of the individuals belonging to the latter species breed in Sweden but leave the country during winter. These species are interesting to include here as they may be more likely to spend the winter at northerly latitudes in a warmer climate. The number of individuals of these species was however very low during the study period.

Methods

BIRD COUNTS

We analysed bird data from a local winter point count route around Storuman (65°06′N 17°07′E) in Swedish Lapland collected between 1986 and 2017. Winter point counts have been one of the methods within the national bird monitoring scheme in Sweden since 1975 (www.fageltaxering.lu.se). The bird data used here was collected as a small part of the national bird monitoring and not specifically for analysing the questions addressed here.

A point count route comprises 20 points, placed at such distance from each other that counting an individual bird twice is prevented or at least minimised. The surveyor choses where to put the route and the points. From each point, the observer counts all birds seen and heard during exactly five minutes. The routes are surveyed up to five times each winter at about the same dates and starting hours every year. Counting periods during winter are October, November, late December or early January, February and March.

The route analysed here has been surveyed on five occasions every winter since 1986. As we wanted to analyse wintering birds breeding in forest habitats, we omitted the data collected in October. During that month there are still varying numbers, sometimes higher numbers, of migrants in the area that do not stay during the winter. Data from the remaining four surveys (November–March) were summed to represent the data for each winter. This means that bird data for the winter of 1986 (which we use to refer to the winter of 1986/1987), consists of data collected from November 1986 to March 1987 and so on. In total, data from 128 surveys between 1986 and 2017 were included.

The same two observers, Håkan Rune and Ulf Andersson, have covered the route every year, although HR has been the main surveyor at all times. The route is a little over 90 km long with the points well spread, see Figure 1. Half or more (10–12 per year) of the points are located near bird feeders. Overall, the number of feeding stations along the route have been rather constant during the period.

FOREST VARIABLES

We compared bird count results with regional forest variables using data from the Swedish National Forest Inventory (SNFI, www.slu.se/centrumbildningar-och-projekt/riksskogstaxeringen), covering Västerbottens Lappmark in which Storuman is situated centrally. The productive forest in Västerbottens Lappmark covers about 18,000 km², that is one third of the overall area of Västerbotten County (54,664 km²). Due to the sampling routine within the SNFI we used five-year moving averages for the forest variables. Hence, forest data representing 1986 in our analyses are actually the average for the five years leading up to 1986, i.e. 1982–1986, and so on. Data from the SNFI covers all productive forest outside of protected areas. We used

four variables representing different successional stages as proxies for forest age. These were the area of open ground without proper forest vegetation (outcrops with very few trees as well as clear-cuts where the forest recently had been removed), young forest (planted forest 0–30 years old), middle-aged forest (forest 30–70 years old) and forest ready for cutting (forest at least 70 years old, but most probably even older in these parts of Sweden). We also included old-growth forest (>140 years of age) area, area of older forest rich in deciduous trees (>80 years old), standing volume of wood, and the volume of hard dead wood per ha as variables.

WEATHER DATA

We correlated bird count results with temperature and precipitation data from Gunnarn weather station, accessed through the Swedish Meteorological and Hydrological Institute (SMHI) open database (http://opendata-download-metobs.smhi.se). Gunnarn weather station is located 4 km from the nearest, and 30 km from the farthest, bird count point.

Based on monthly average values, we calculated mean annual values for the period April–March. The annual mean value for 1986 was hence calculated from temperatures in April 1986 through March 1987. Summer mean temperatures were calculated for the period April to August each year, and winter temperatures for the period November to March each winter. We calculated mean precipitation values in the same way. There was no data for February 1992 from Gunnarn. In this case, we used data from the now closed (2004) weather station in Stensele instead, which is located even closer to the points on the route (1 km from the nearest, and 24 km from the farthest, bird count point). The weather station in Gunnarn was moved a short distance in 2013, it is now situated 29 meters higher in altitude than before. This may affect both temperature and precipitation somewhat, but should not change any overall patterns.

ANALYSES

We analysed changes in bird abundance and species richness as well as forest and weather variables during the period with Spearman's rank correlations (Spearman 1904, Daniel 1990). We also used Spearman's rank correlations to analyse bird abundance, as well as species richness, in relation to forest and weather variables. All statistical analyses were performed in Excel 2016.
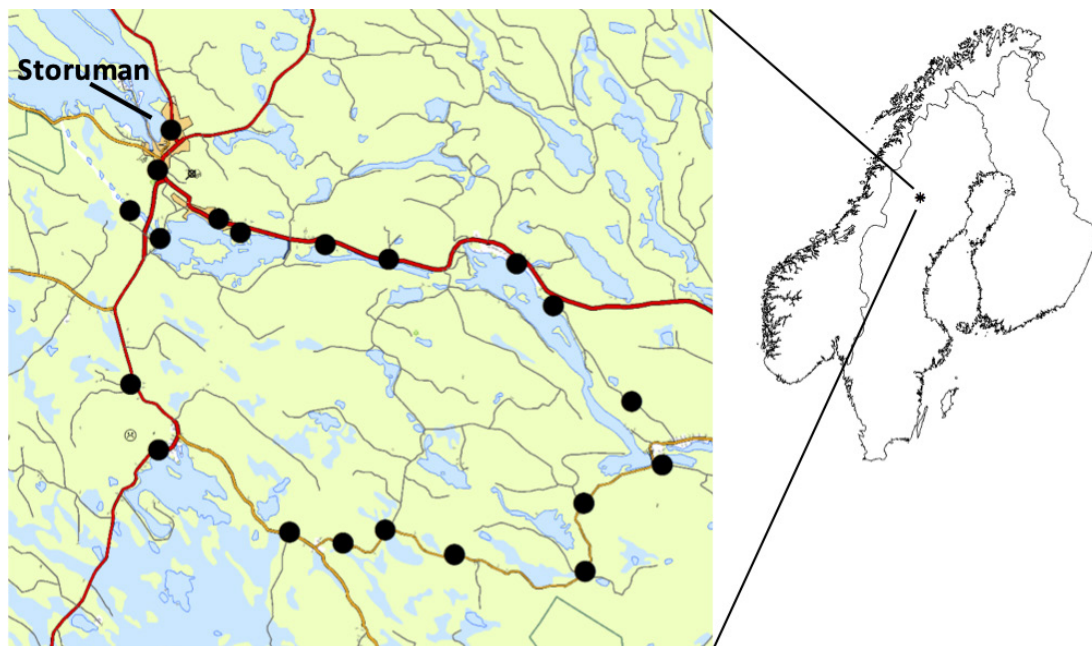
FIGURE 1. Map of the bird survey route (left) and where the route is situated in the northern part of Sweden (right). At each point (black dot), all observed birds were counted during five minutes during each survey.
— *Karta över den aktuella punktrutten (till vänster) och ruttens läge i norra delen av Sverige (till höger). Vid varje punkt (svart prick) räknades alla observerade fåglar under fem minuter vid varje inventering.*

In our analyses, we looked at birds directly connected to forest habitats during the breeding season, hereafter forest birds. These birds may or may not use forest habitats during the winter. We do not analyse winter habitat use, and winter habitat use is not relevant for the questions we ask here. We classified forest birds in the same way as Ram *et al.* (2017). In our case, this meant that we initially classified 35 species observed along the route as forest birds (see Appendix 1). Here we lumped all identified Red and Parrot Crossbills *Loxia curvirostra* and *Loxia pytyopsittacus* together with unidentified Red/Parrot Crossbills into one taxon, i.e. Crossbills, in order to minimize possible effects of the identification pitfalls regarding this group of birds (see Martin *et al.* 2019). In addition, we included two raptors (Golden Eagle *Aquila chrysaetos* and Northern Goshawk *Accipiter gentilis*) and two owls (Northern Hawk-Owl *Surnia ulula* and Eurasian Pygmy Owl *Glaucidium passerinum*) among the forest birds. Hence, the group of forest birds comprised 39 species in total (Appendix 1).

We also analysed a group of forest specialist species. They are connected to more varied and natural forests with a high degree of structural complexity (see Ottvall *et al.* 2008). There are nine forest specialist species that has been seen at least once along the route: Western Capercaillie *Tetrao urogallus*, Black Woodpecker *Dryocopus martius*, Lesser Spotted Woodpecker *Dryobates minor*, Eurasian Three-toed Woodpecker *Picoides tridactylus*, Willow Tit *Poecile montanus*, Grey-headed Chickadee *Poecile cinctus*, Eurasian Treecreeper *Certhia familiaris*, Siberian Jay *Perisoreus infaustus* and Pine Grosbeak *Pinicola enucleator*.

In addition to analysing the bird data as they were counted in the field, we calculated the Community Temperature Index (CTI; Devictor *et al.* 2008) for each winter, and then analysed changes in CTI over the period as well as correlations between CTI and weather variables. CTI is a measure of the composition of the bird community, here at the local level as we base the calculations on forest bird numbers counted along the single route involved. CTI can be calculated for any geographical area, such as route, province or country, as long as you have data covering the whole bird community or a representative sample of the whole bird

community. CTI shows changes in the relative abundances of birds with colder or warmer distributions. If birds with warmer distribution areas become relatively more common, CTI will increase. If birds with colder distribution areas become relatively more common, CTI will decrease. Hence, CTI shows changes in bird community composition (Devictor *et al.* 2008)

CTI is calculated as the average Species Temperature Index (STI) of all bird individuals (observed ones or estimated total population sizes). The STI, in turn, is the average temperature during the breeding season in the European breeding area of the species. Here we used the average temperature during April–August, in turn averaged over the period 1961–2008 for the breeding distribution of each species. We used temperature data from the Worldclim database (http://www.worldclim.org) and breeding distributions from the European breeding bird atlas (Hagemeijer & Blair 1997) in our calculations of STI. A species with a northern breeding distribution will have a relatively low STI. A species with a southern distribution will have a relatively higher STI. For more details, see Devictor *et al.* (2008) and Lindström *et al.* (2013). We calculated a CTI for the route for each winter based on the total number of

forest bird individuals observed during the four periods. CTI is expressed in degrees Celsius (°C).

Results

CHANGES IN BIRD ABUNDANCE AND BIRD COMMUNITY COMPOSITION

Over the years, 39 different forest bird species were observed along the route. The number of registered forest bird species per winter increased during the period (Figure 2, r_s=0.50, p<0.01). There were a few new forest species turning up in the area during the study period. Among these were the Eurasian Nuthatch *Sitta europea*, seen for the first time in 1995 and observed annually since 2007; the Grey-headed Woodpecker *Picus canus*, not seen until 2002 but seen during most years thereafter; and Spotted Nutcracker *Nucifraga caryocatactes*, first seen in 2008 and since then observed during several years. There were no forest species that disappeared from the area during the study period.

A total of 15,907 forest bird individuals were observed over the years. Total numbers of observed forest birds along the route per winter are shown in Appen-
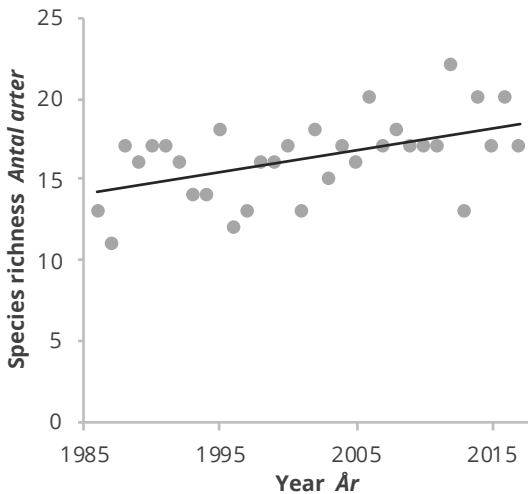
FIGURE 2. Number of forest bird species observed along the route per winter (total number during four surveys per winter, November–March) 1986–2017. The trend line represents a linear regression (though analyses are made with non-parametric correlations).
— *Antal observerade skogsfågelarter längs rutten per vinter (fyra inventeringar / vinter, nov–mar) 1986–2017. Trendlinjen visar en linjär regression (fast analyserna är gjorda med icke-parametrisk korrelation).*
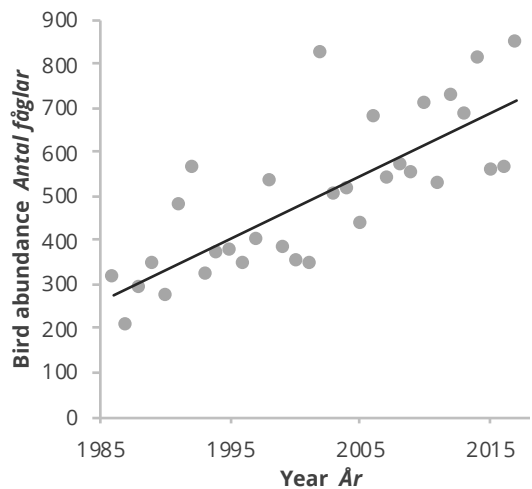
FIGURE 3. Bird abundance along the route per winter (sum of four surveys per winter, November–March) 1986–2017. The trend line represents a linear regression (though analyses are made with non-parametric correlations).
— *Totala antalet fågelindivider av de utvalda skogsfågelarterna längs rutten per vinter (summan av fyra inventeringar per vinter, november–mars) 1986–2017 (fast analyserna är gjorda med icke-parametrisk korrelation).*
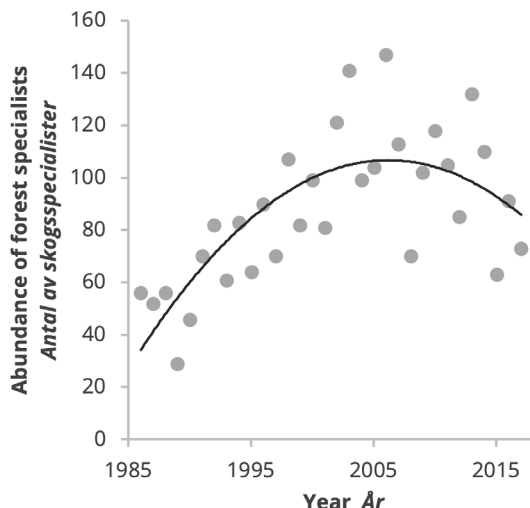
FIGURE 4. Abundance of forest specialist species counted along the route per winter (sum of four surveys per winter, November–March) 1986–2017. The trend line represents a quadratic function (though analyses are made with non-parametric correlations).
— *Totalantalet individer av specialiserade skogsfågelarter längs rutten per vinter (fyra inventeringar per vinter, november–mars) 1986–2017. Trendlinjen visar en kvadratisk funtion (fast analyesrn är gjorda med icke-parametrisk korrelation).*

FIGURE 5. Average Community Temperature Index (CTI) per winter along the route 1986–2017. The trend line represents a linear regression (though analyses are made with non-parametric correlations).
— *Fågelsamhällets genomsnittliga temperaturindex (CTI) per vinter längs rutten 1986–2017. Trendlinjen visar en linjär regression (fast analyserna är gjorda med icke-parametrisk korrelation).*
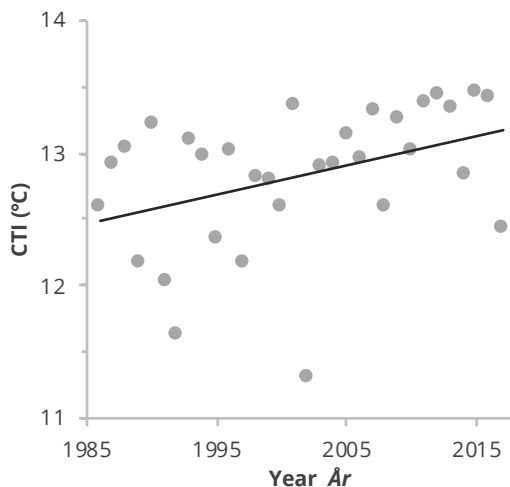
dix 1. The abundance of observed forest birds increased significantly 1986–2017 (Figure 3, $r_s = 0.81$, $p < 0.001$). The most common forest birds observed along the route were Great Tit *Parus major*, Eurasian Bullfinch *Pyrrhula pyrrhula*, Willow Tit, and Bohemian Waxwing *Bombycilla garrulus*. These species were all observed with more than 1,000 individuals in total during the period, and made up 58–88 % of all observed forest birds per winter. The proportions between the most common species and the less common species varied between years, but for the entire period the proportions did not change. We found increasing numbers of the four most common species ($r_s = 0.82$, $p < 0.001$), and the remaining 35 of the less common species also increased ($r_s = 0.37$, $p < 0.05$).

Between two and six forest specialist species were seen along the route every winter. During the whole period we found no significant change in the number of forest specialist species ($r_s = 0.01$, $p > 0.10$) Willow Tit was by far the most common specialist bird and the only one observed every year. Siberian Jay was observed every year except one (2014). The other specialist species were observed more irregularly. In total, the number of forest specialist birds increased sharply from 1989 to 2006, but has since decreased in numbers

again. However, seen over the whole study period, the number of forest specialist birds has increased (Figure 4, $r_s = 0.58$, $p < 0.01$).

Bird community composition, measured as average CTI per winter, varied between 11.3 °C and 13.5 °C. CTI increased significantly over the study period (Figure 5, $r_s = 0.44$, $p < 0.05$). This means that the proportions of forest bird individuals belonging to species with warmer breeding distributions became relatively more common during the 32 study winters compared to forest birds belonging to species with colder breeding distributions.

CHANGES IN EXTERNAL FACTORS

Forest variables

We show Spearman's rank correlations between forest variables in Västerbottens lappmark and time over the period 1986–2017 in Table 1. We found decreasing areas of open ground and young forest, while the area of more fully grown forest increased. This increase mainly regarded middle-aged forest (30–70 years of age), while the area of forest ready for clear-cutting (>70 years old) decreased. The old-growth forest (>140 years) area decreased during the first ten years, followed by an

TABLE 1. Spearman's rank correlations between forest variables and year for Västerbottens lappmark 1986–2017. r_S is the Spearman's rank correlation coefficient. Statistical significance (sign.) is indicated by asterisks, where * p<0.05, ** p<0.01, *** p<0.001.
— *Spearmans rangkorrelationer mellan skogsvariabler och år för Västerbottens lappmark 1986-2017. r_S är Spearmans rangkorrelationskoefficient. Statistisk signifikans (sign.) visas av asterisker där * p<0,05, ** p<0,01, *** p<0,001.*

Forest variable *Skogsvariabel*	r_S	Sign.
Open ground, area *Öppen mark, yta*	–0.95	***
Young forest (0–30 years), area *Ung skog (0–30 år), yta*	–0.62	***
Middle-aged forest (30–70 years), area *Medelålders skog (30–70 år), yta*	0.95	***
Forest ready for cutting (>70 years), area *Avverkningsmogen skog (>70 år), yta*	–0.80	***
Fully grown forest (middle-aged + ready for cutting; >30 years), area *Fullt uppvuxen skog (medelålders + avverkningsmogen; >30 år), yta*	0.41	*
Old forest (>140 years), area *Gammal skog (>140 år), yta*	0.43	*
Older forest, rich in deciduous trees (>80 years), area *Äldre lövträdsrik skog (>80 år), yta*	–0.68	***
Standing volume of wood in fully grown forest *Stående skogsvolym i fullt uppvuxen skog*	0.96	***
Dead wood, volume *Död ved, volym*	0.87	***

increase during the next ten years, and finally remaining at about the same level in the end of the period, resulting in a slight overall increase over the whole period. During the study period the area of older forest (>80 years old) rich in deciduous trees decreased, while the standing volume of wood increased continuously, i.e. the forests became denser. The volume of dead wood also increased during the period.

Weather variables

We found no significant changes in local average temperature or precipitation during the period 1986–2017, irrespective of whether we analysed annual, winter, or summer averages (Table 2).

CORRELATIONS BETWEEN BIRDS AND EXTERNAL FACTORS

Birds and forest variables

We found stronger correlations between bird variables and forest variables than between bird variables and weather variables (Appendix 2). The most relevant relationships between bird variables and external factors are shown in Figure 6.

The forest species richness significantly increased with increasing area of middle-aged forest, standing volume of wood, volume of dead wood and increasing area of old-growth forest, but significantly decreased with increasing area of open ground and forest ready

for cutting, and tended to do so for older forest rich in deciduous trees (Figure 6, Appendix 2).

The pattern was similar for abundance of forest birds, which significantly increased with area of middle-aged forest, standing volume of wood, and volume of dead wood, but significantly decreased with increasing area of open ground, forest ready for cutting, and older forest rich in deciduous trees (Figure 6, Appendix 2). We found a tendency for an increased number

TABLE 2. Spearman's rank correlations between weather variables from Gunnarn and year 1986–2017. r_S is the Spearman's rank correlation coefficient. The Spearman's rank correlation was not statistically significant for any of the weather variables.
— *Spearmans rangkorrelationer mellan vädervariabler från Gunnarn och år 1986–2017. r_S är Spearmans rangkorrelationskoefficient. Ingen av vädervariablerna uppvisade en statistiskt signifikant korrelation med år.*

| Weather variable *Vädervariabel*	r_S
Annual temperature (April–March) *Årstemperatur (april–mars)*	0.18
Winter temperature (November–March) *Vintertemperatur (november–mars)*	0.05
Summer temperature (April–August) *Sommartemperatur (april–augusti)*	0.18
Annual precipitation (April–March) *Årsnederbörd (april–mars)*	–0.10
Winter precipitation (November–March) *Vinternederbörd (november–mars)*	–0.25
Summer precipitation (April–August) *Sommarnederbörd (april–augusti)*	–0.08
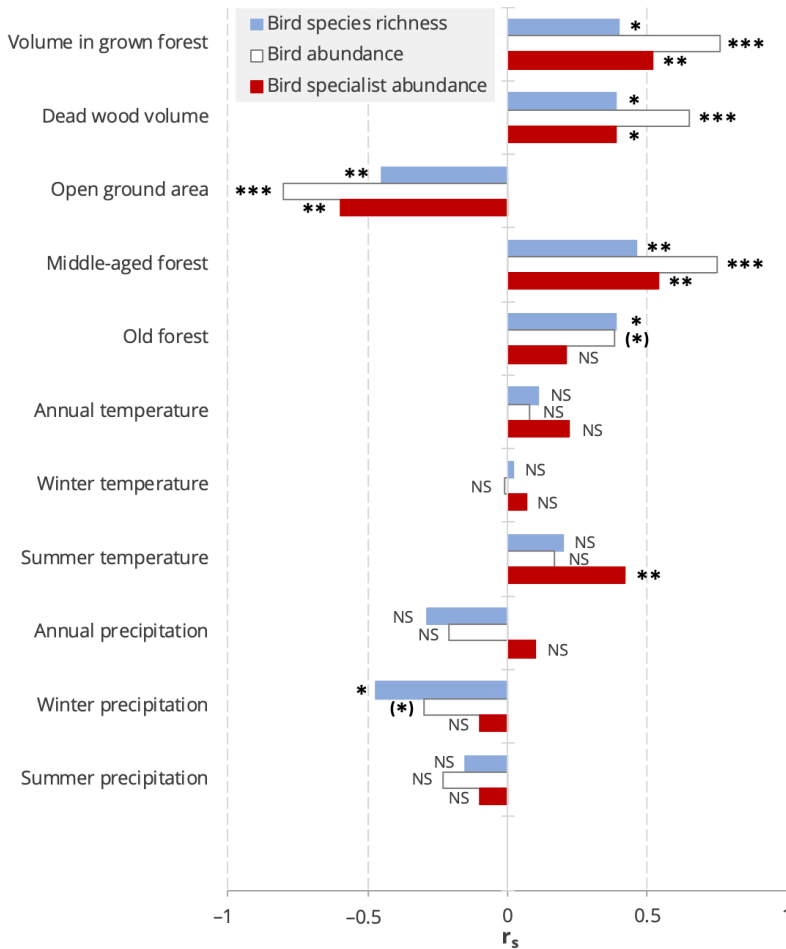
FIGURE 6. Spearman's rank correlations between bird variables and external factors. r_s is the Spearman's rank correlation coefficient. Statistical significance is shown by asterisks where * p<0.05, ** p<0.01, *** p<0.001. (*) indicates tendencies that were not statistically significant but with p<0.10. NS=not significant.
— *Spearmans rangkorrelationer mellan fågelvariabler och yttre faktorer. r_s är Spearmans rangkorrelationskoefficient. Statistisk signifikans visas av asterisker där * p <0,05, ** p <0,01, *** p <0,001. (*) indikerar tendenser som inte är statistiskt signifikanta, men med p <0,10. NS=inte signifikant.*

Birds and weather variables
We found no significant correlations between temperature and wintering forest bird individuals or number of forest bird species in general, regardless of whether we looked at average annual, winter, or summer temperatures. However, higher summer temperatures significantly correlated with an increase of the numbers of forest specialists (Figure 6, Appendix 3).

Annual and summer precipitation did not affect wintering bird numbers along the route. The specialists did not show any significant correlations with precipitation, but the number of forest bird species increased significantly and the forest bird abundance showed a tendency to increase when winter precipitation decreased (Figure 6, Appendix 3).

Bird community composition
We found no significant correlations between CTI and observed numbers of forest species, forest specialists, or abundance (all r_s

of forest birds with increasing area of old-growth forest (Figure 6, Appendix 2).

The abundance of forest specialist birds significantly increased with increasing area of middle-aged forest, standing volume of wood, and volume of dead wood, but significantly decreased with increasing area of open ground, forest ready for cutting, and older forest rich in deciduous trees. Somewhat surprisingly, the numbers of forest specialist birds did not increase with increasing area of old-growth forest (Figure 6, Appendix 2).

0.02–0.10). In general, CTI did not show any significant correlations with weather variables, save for winter precipitation, where increased precipitation correlated with decreased CTI (Table 3).

Discussion
The main driving force behind the recent decades' increase in forest birds in Sweden is uncertain. We addressed this question from a local perspective by

measuring winter bird abundance on a local route, while looking at forest composition at a regional level. The forest development may not be exactly the same at a regional level as around the local bird route. However, changes in forest composition at a regional level should affect the bird numbers at a regional level, which to a large extent should affect local bird numbers along the survey route analysed here. Also, winter bird assemblages are most probably recruited from a larger area in the region than just locally around the actual route. Hence, there is no reason to expect that the different geographical scales for bird and forest data should drastically affect the relationships that we found.

We found that increased wintering forest bird numbers around Storuman in Swedish Lapland show stronger correlations with forest variables than with local average weather variables. At least the local weather variables we explored here did not explain the increased abundance of forest birds, neither average temperature nor precipitation. It might be that there are other weather variables that show stronger correlations with bird data, and that is something that could be addressed in coming analyses. Further, just as regional forest development data may be advantageous because of a larger recruitment area of wintering birds, using regional weather data could possibly paint a different picture. There are however no signs of that the weather at Gunnarn should be any different from the regional weather.

Some of the correlations found between forest birds and forest parameters probably have little biological significance. For example, that reduced area of older forest rich in deciduous trees would have been positive for forest birds in general is highly unlikely. Older forest rich in deciduous trees is known to be rich in birds, both in terms of number of species and abundance (Svensson *et al.* 1999, Poulsen 2002, Forslund 2003, Tjernberg and Svensson 2007, Rosenvald *et al.* 2011). On the other hand, the correlations between forest birds and decreasing areas of open ground and increasing volume of dead wood are likely to be biologically significant (Svensson *et al.* 1999, Poulsen 2002, Forslund 2003, Tjernberg and Svensson 2007, Rosenvald *et al.* 2011). The fact that the volume of dead wood is increasing is probably positive for the forest birds, as well as for biodiversity in general; several of the here recorded forest birds find nesting sites in dead wood and/or find their food in dead wood. A decreased area

TABLE 3. Spearman's rank correlations between Community Temperature Index (CTI) and weather variables 1986–2017. r_s is the Spearman's rank correlation coefficient. Statistical significance (sign.) is shown by asterisks where * p<0.05, ** p<0.01, *** p<0.001. NS=not significant.
— *Spearmans rangkorrelationer mellan fågelsamhällets temperaturindex (CTI) och vädervariabler 1986–2017. r_s är Spearmans rangkorrelationskoefficient. Statistisk signifikans visas av asterisker där * p <0,05, ** p <0,01, *** p <0,001. NS=inte signifikant.*

Weather variable *Vädervariabel*	r_s	Sign.
Annual temperature (April–March) *Årstemperatur (april–mars)*	0.18	NS
Winter temperature (November–March) *Vintertemperatur (november–mars)*	0.07	NS
Summer temperature (April–August) *Sommartemperatur (april–augusti)*	0.24	NS
Annual precipitation (April–March) *Årsnederbörd (april–mars)*	–0.27	NS
Winter precipitation (November–March) *Vinternederbörd (november–mars)*	–0.36	*
Summer precipitation (April–August) *Sommarnederbörd (april–augusti)*	–0.20	NS

of open ground means that the area of forest is increasing, hence it seems obvious that this is beneficial for species connected to forest. Denser forests, though, are not always positive for forest birds, but the more open older forests, that were harvested in the 1950s to 1970s in southern Lapland, are now considerably denser middle-aged managed forests, which may be more suitable for some of the forest bird species.

Forest bird community composition, measured as CTI, changed significantly during the study period. This means that birds with warmer distribution did relatively better than birds with colder breeding distributions. Despite this we did not find any correlations between CTI and local temperature. This is at odds with the general finding that bird community composition at local and national level can change relatively rapidly in relation to changes in temperature (Devictor *et al.* 2008, Godet *et al.* 2011, Lindström *et al.* 2013, Lehikoinen *et al.* 2016, Lindström 2018).

Local species richness shows the same pattern as Haas *et al.* (2014) found for breeding bird species at a national scale. They showed that the number of breeding species has increased continuously in Sweden since 1850. This finding is also in line with predictions that the number of breeding birds should decrease in southern Europe, but increase in more northerly areas

due to the ongoing global warming (Barbet-Massin *et al.* 2012, Lehikoinen & Virkkala 2016, Virkkala & Lehikoinen. 2017). There are, however, probably no direct links between the expectations of increasing numbers of breeding species in Sweden and northern Europe at large, and our finding of an increasing number of wintering forest species locally in southern Lapland, since none of the forest species recorded along the route and included in this analysis are new in the Swedish breeding bird fauna. On the other hand, there could be such links at a more local level, i.e. if forest species previously not breeding in the region have established themselves there during the study period. This is partly supported by our data, where some forest species that were not seen during the early winters of our study were seen on a more regular basis during later years. All these species—Eurasian Nuthatch, Grey-headed Woodpecker, and Spotted Nutcracker—probably established themselves as breeding birds in the local or regional area during the study period. Hence, part of the increase in wintering forest bird species around Storuman is probably caused by an increased number of breeding forest bird species in the area.

The local development of wintering forest bird numbers around Storuman in general follow a similar pattern in Sweden as a whole during the last two decades. In total, the number of breeding bird individuals has increased in Sweden since 1998 (Green *et al.* 2019). Most of this increase has taken place among forest birds, while the number of individuals of species linked to agricultural areas, wetlands, coasts and mountains either decreased or remained more or less stable during the same period. It may be that the general increase of forest birds mirrors the decline among bird species linked to cultivated areas. The areas of farmland and pastures have steadily declined, and become forested as farming has ceased (Wretenberg *et al.* 2006). Another related explanation may be the general decrease in human population in northern rural areas. Storuman Municipality showed a population decrease of 27.2 % during 1986–2017 (www.scb.se). Exactly how this decrease in local human population may have affected the local abundance of wintering forest birds remains unsure, but we can think of two different ways, apart from that smaller and smaller areas are kept open for farming. (1) A decrease in local human population size could have been beneficial for abundance of forest birds, as general

and direct human pressure on the local environment decreases with fewer people around. Or it could work in an opposite way for wintering forest birds if (2) local wintering populations are more or less dependent on feeding stations provided by humans. We do not know the exact development of the number of bird feeding stations or the amount of bird food provided around Storuman during the period. Although the number of stations along the route has remained relatively similar during the period, this may or may not have been the same at a more general level in the area.

We also found increasing numbers of forest specialist birds, although there was actually a sharp increase for the first 20 years followed by a decrease during the last 12 years. The local forest specialist birds follow the national patterns fairly well. In Sweden, the number of forest specialist birds increased in 1998 to 2008, but in the last decade the positive trend has leveled off (Green *et al.* 2019). At the national level the positive effects of important forest parameters such as increasing area of old-growth forest, stratification, number of retention trees per ha, and dead wood volume appear to have ceased recently (Ram *et al.* 2017). In our study the numbers of forest specialist birds increased with increasing middle-aged forest area, standing wood volume and dead wood volume. Somewhat surprisingly, the abundance of forest specialist birds did not increase with increased old-growth forest area. Despite the fact that forest specialist birds locally did not increase with increased old-growth forest area, the future development of forest specialist birds, both locally and in Sweden at large, may be dependent on what happens to the structurally complex forests that still remain.

Our main finding is that forest bird numbers correlate more strongly with the development of the forest than with changes in local weather. However, there could be other factors at play that also vary on a time scale similar to the variation in bird numbers. We already discussed reduced agriculture and decreasing human population as potential factors; another variable that could possibly affect the variation in bird numbers is the annual strength of the photosynthesis. There is increasing support for the notion that a warmer climate and a fertilizer effect from the increasing CO_2 levels in the atmosphere have made a large part of the planet greener (Keeling *et al.* 1996, Los 2013, Zhu *et al.* 2016, Munier *et al.* 2018, Fernández-Martínez *et al.* 2019). A

sign of increasing photosynthesis at high latitudes is that the seasonal amplitude of CO_2 concentrations has risen around 25 % since the 1960s, mainly due to higher temperatures (Forkel *et al.* 2016). If, or how, this affects the birds in some way is unknown, but might be worth to study in detail. Increasing photosynthesis will lead to more vegetation, which could lead to higher densities and numbers of primary consumers such as insects. This, in turn, would potentially provide more food for birds during the northern breeding season, resulting in higher breeding success and higher bird numbers also among wintering forest bird species.

In conclusion, since neither the average temperature nor the average precipitation has changed during the study period, these variables are less likely to explain the general increase of wintering forest birds around Storuman. However, we found strong correlations between variables measuring forest birds and denser, fully grown forests, volumes of dead wood, and decreased areas of open ground without forest vegetation. While there may be other explanations behind the increase in forest bird numbers, such as reduced agriculture, decreased human population, or stronger photosynthesis, our results indicate that local land use has been favourable for forest birds in recent decades in this area.

Acknowledgements

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Svensk sammanfattning

De senaste decennierna har antalet fåglar knutna till skogsmiljö i Sverige ökat. Anledningen till detta är inte helt klarlagd. Ökningar av ytan skog och av tillgången på skogsstrukturer viktiga för biologisk mångfald, samt ett varmare klimat, har alla föreslagits som möjliga och troliga förklaringar. Här undersöker vi denna fråga lite närmare genom att jämföra fågeldata från en lokal vinterpunktrutt runt Storuman i Lappland mellan 1986 och 2017, med regionala skogs- och lokala väderdata.

Regionalt sett minskade ytan av öppen mark och yngre skogar under de senaste årtiondena. Samtidigt ökade ytan med uppvuxen skog, något som främst be-rodde på en ökning av ytan gallringsskog, medelålders skog på mellan 30 och 70 år. Ytan avverkningsmogen skog, >70 år gammal, minskade i stället något. Ytan gammal skog, >140 år gammal, ökade totalt sett. I mer detalj skedde en minskning de första tio åren, följt av en ökning under följande tio åren, varefter ingen större förändring skedde. Volymen av uppvuxen skog ökade, dvs. skogen blev allt tätare och även mängden död ved ökade (Tabell 1). Något förvånande skedde inga förändringar av lokala års-, vinter- eller sommarmedelvärden för temperatur och nederbörd under perioden (Tabell 2).

Antalet observerade arter och individer per år av övervintrande fåglar, som under häckningstiden är knutna till skogsmiljö, ökade runt Storuman mellan 1986 och 2017 (Figur 2 och Figur 3). Sammantaget ökade också antalet individer per år av mer specialiserade skogsarter (Figur 4).

En del av ökningen av antalet observerade arter hänger ihop med att några nya arter etablerade sig i området under studieåren. Nötväckan *Sitta europaea* sågs för första gången 1995 och har observerades årligen sedan 2007. Gråspetten *Picus canus* dök upp först 2002 och har sedan setts nästan varje år. Nötkråkan *Nucifraga caryocatactes* har visat sig flera gånger sedan 2008, då den observerades första gången. Det var inga arter som försvann från området under perioden. Antalet arter visade signifikant positiva samband med ökande yta medelålders skog, stående skogsvolym, volymen död ved och ytan gammal skog, men negativa sådana med ytan kalmark, slutavverkningsmogen skog, och äldre lövrik skog (Figur 6).

Totalt sett registrerades 15 907 fåglar av skogsanknutna arter genom åren. De vanligaste arterna var talgoxe *Parus major*, domherre *Pyrrhula pyrrhula*, sidensvans *Bombycilla garrulus* och talltita *Poecile montanus*. Dessa fyra har var för sig setts i mer än 1 000 exemplar totalt. Både de allra vanligaste arterna och de mindre vanliga arterna ökade i antal. De vanligaste arternas andel av det totala antalet sedda fåglar varierade mycket mellan åren, men ingen statistiskt säker förändring i denna andel skedde sett över hela perioden. I absoluta tal ökade dock de vanligaste fåglarna mer än de mindre vanliga. Antalet skogsfågelindivider ökade med ökande yta medelålders skog, stående skogsvolym, och volymen död ved, men minskade i antal med ökad yta kalmark, slutavverkningsmogen skog och äldre lövrik skog. Vi fann en tendens till ökat antal skogsfåglar när ytan gammal skog ökade (Figur 6, Bilaga 2).

Av de mer specialiserade skogsarterna, som ställer högre krav på skogens struktur, var talltita den överlägset vanligaste arten och den enda arten som observerades varje år. Lavskrika *Perisoreus infaustus* observerades alla år utom ett (2014). De andra skogsspecialistarterna observerades mer oregelbundet. Skogsspecialisterna ökade kraftigt de första 20 åren följt av en minskning under de senaste tolv åren, vilket speglar utvecklingen i Sverige som helhet väl. Sett till hela perioden ökade dock antalet skogsspecialister signifikant (Figur 4). Vi fann ökande antal skogsspecialister med ökande yta medelålders skog, stående skogsvolym, och mängden död ved, men minskande antal med ökande yta kalmark, slutavverkningsmogen skog och äldre lövrik skog. Något överraskande ökade antalet skogsspecialister inte med ökad yta gammal skog (Figur 6).

Sammansättningen i vinterfågelsamhället av skogsanknutna arter kring Storuman, uttryckt som fågelsamhällets temperaturindex (Community Temperature Index, CTI), visade att skogsanknutna fåglar arter med varmare utbredningsområden under häckningstid blev relativt sett vanligare jämfört med skogsfåglar som tillhör arter med kallare häckningsområden under de 32 åren (Figur 5). CTI visade dock inga samband med antalet observerade skogsfåglar. CTI visade inte heller några generella samband med väder, annat än att CTI ökade med minskande mängd vinternederbörd (Tabell 3).

Sammanfattningsvis kan sägas att eftersom varken medeltemperatur eller medelnederbörd förändrades under studieperioden kan dessa variabler inte förklara den allmänna ökningen av vinterfåglar av skogsanknutna arter runt Storuman. För de ökande antal individer, arter och skogspecialister hittade vi i stället tydliga korrelationer med ytan uppvuxen – främst medelålders – skog, tätare uppvuxna skogar, ökad volym död ved och minskade områden med öppen, nyligen avverkad, mark och ungskog. Även om det kan finnas andra förklaringar bakom det ökande antalet skogsfåglar, såsom minskat jordbruk, minskande lokalbefolkning eller starkare fotosyntes, tyder våra resultat på att regional markanvändning runt Storuman har varit gynnsam för skogsfåglar under de senaste årtiondena.

Appendix 1. Annual count data

English name *Engelskt namn*	Swedish name *Svenskt namn*	Scientfic name *Vetenskapligt namn*	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Golden Eagle	kungsörn	*Aquila chrysaetos*	1									3						1	
Northern Goshawk	duvhök	*Accipiter gentilis*					1				1				1				
Black Grouse	orre	*Lyrurus tetrix*	20	6	2	21	12	9	11	5	34	26	39	8	52	18	10	13	69
Western Capercaillie	tjäder	*Tetrao urogallus*									1				1		1		1
Hazel Grouse	järpe	*Tetrastes bonasia*	5				3	1		2	1	1				2			8
Northern Hawk Owl	hökuggla	*Surnia ulula*				1	3												
Eurasian Pygmy Owl	sparvuggla	*Glaucidium passerinum*						1		1				1			1		
Grey-headed Wood-pecker	gråspett	*Picus canus*						1											2
Great Spotted Wood-pecker	större hackspett	*Dendrocopus major*	9		15	6	4	6	5	6	1		3	3	5	3	4	4	6
Lesser Spotted Woodpecker	mindre hackspett	*Dendrocopus minor*																	
Eurasian Three-toed Woodpecker	tretåig hackspett	*Picoides tridactylus*			3		2		1										
Black Woodpecker	spillkråka	*Dryocopus major*			1		2									1		1	
Northern Raven	korp	*Corus corax*	9	4	17	22	9	64	16	8	16	13	14	8	60	7	12	19	23
Spotted Nutcracker	nötkråka	*Nucifraga caryocatactes*																	
Eurasian Jay	nötskrika	*Garrulus glandarius*	8	6	9	3	7	7	9	2	4	3	5	2	8	6	5	7	11
Siberian Jay	lavskrika	*Perisoreaus infaustus*	10	1	6	4	3	6	4	6	5	8	11	5	11	3	4	5	9
Long-tailed Tit	stjärtmes	*Aegithalos caudatus*			2														
Great Tit	talgoxe	*Parus major*	92	73	98	82	143	115	143	104	139	98	144	121	178	125	117	164	129
Eurasian Blue tit	blåmes	*Cyanistes caeruleus*	6	5	9	5	1	7	10	7	11	9	9	8	3	12	10	10	18
Coal Tit	svartmes	*Periparus ater*					6	6	9	6	2				2		1	1	2
Grey-headed Chickadee	lappmes	*Poecile cinctus*					2			1							1	2	
Willow Tit	talltita	*Poecile montanus*	43	51	43	24	39	65	75	59	69	57	79	65	95	79	93	75	73

APPENDIX 1 continued | *Appendix 1 fortsatt.*

| Species *Art* | | | | | | | | | | | | | | | | | | |
English name *Engelskt namn*	Swedish name *Svenskt namn*	Scientfic name *Vetenskapligt namn*	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	**Sum**
Golden Eagle	kungsörn	*Aquila chrysaetos*		3		1	1				1				1	1		13
Northern Goshawk	duvhök	*Accipiter gentilis*							1									4
Black Grouse	orre	*Lyrurus tetrix*	6	12	6	1	11	69	28	19	23	3	1		3	8	9	554
Western Capercaillie	tjäder	*Tetrao urogallus*				2	1		1		2	1			1	1		13
Hazel Grouse	järpe	*Tetrastes bonasia*	6	2		1	1	6		2	1	2		1	2		1	48
Northern Hawk Owl	hökuggla	*Surnia ulula*		1							1		2					8
Eurasian Pygmy Owl	sparvuggla	*Glaucidium passerinum*				1	1											6
Grey-headed Woodpecker	gråspett	*Picus canus*		3		1	3	6	3	4	1	2	2	2	1			31
Great Spotted Woodpecker	större hackspett	*Dendrocopus major*	7	15	16	22	7	23	14	23	14	8	16	19	33	6	10	313
Lesser Spotted Woodpecker	mindre hackspett	*Dendrocopus minor*											1					1
Eurasian Three-toed Woodpecker	tretåig hackspett	*Picoides tridactylus*	1		1					2				1				11
Black Woodpecker	spillkråka	*Dryocopus major*	1	1		2	1		2					1				13
Northern Raven	korp	*Corus corax*	14	28	10	28	43	9	14	21	16	17	18	16	15	11	16	597
Spotted Nutcracker	nötkråka	*Nucifraga caryocatactes*						2		1		15	2		1			21
Eurasian Jay	nötskrika	*Garrulus glandarius*	5	8	9	17	14	5	4	15	10	15	17	9	11	9	12	262
Siberian Jay	lavskrika	*Perisoreaus infaustus*	10	7	12	10	12	9	7	4	5	6	4		5	1	8	201
Long-tailed Tit	stjärtmes	*Aegithalos caudatus*				12							15					29
Great Tit	talgoxe	*Parus major*	169	190	142	229	179	127	208	255	212	286	241	271	202	229	206	5,211
Eurasian Blue tit	blåmes	*Cyanistes caeruleus*	14	11	26	29	36	29	35	37	38	35	41	32	36	36	22	597
Coal Tit	svartmes	*Periparus ater*	4	2		1	1	1	1			1		2	1		1	50
Grey-headed Chickadee	lappmes	*Poecile cinctus*																6
Willow Tit	talltita	*Poecile montanus*	110	93	93	136	100	66	96	113	98	77	128	104	60	88	64	2,510

APPENDIX 1 continued | *Appendix 1 fortsatt.*

Species *Art*																				
English name *Engelskt namn*	Swedish name *Svenskt namn*	Scientfic name *Vetenskapligt namn*	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Eurasian Nuthatch	nötväcka	*Sitta europea*										2				1			
Eurasian Treecreeper	trädkrypare	*Certhia familiaris*			1							1			1				
Mistle Thrush	dubbeltrast	*Turdus viscivorus*																	1
Fieldfare	björktrast	*Turdus pilaris*		2		1		2	6	1		4	2	8	1	19	12		3
Redwing	rödvingetrast	*Turdus iliacus*						2				1							
Common Blackbird	koltrast	*Turdus merula*																	
Eurasian Blackcap	svarthätta	*Sylvia atricapilla*		1															
Goldcrest	kungsfågel	*Regulus regulus*			2				2						1				
Bohemian waxwing	sidensvans	*Bombycilla garrulus*		13	11	43	9	121	155			13	2	81	28	27	39		232
Hawfinch	stenknäck	*Coccothraustes coccothraustes*				2													
Eurasian Siskin	grönsiska	*Carduelis spinus*				2													
Eurasian Bullfinch	domherre	*Pyrrhula pyrrhula*	46	43	68	69	25	62	39	112	74	60	36	82	84	73	40	45	182
Pine Grosbeak	tallbit	*Pinicola enucleator*	3		4	2			5		10	1	1		2		1		41
Red / Parrot Crossbill	mindre / större korsnäbb	*Loxia curvirostrata / pytopsittacus*	62		1	56		5	70			75		6		2	3		12
Two-barred Crossbill	bän-delkorsnäbb	*Loxia leucoptera*										3							
Common chaffinch	bofink	*Fringilla coelebs*																	
Brambling	bergfink	*Fringilla montifringilla*																	
Total	**totalt**		314	205	292	343	271	480	560	320	368	378	345	398	532	379	354	347	822

APPENDIX 1 continued | *Appendix 1 fortsatt.*

English name / *Engelskt namn*	Swedish name / *Svenskt namn*	Scientfic name / *Vetenskapligt namn*	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	**Sum**
Eurasian Nuthatch	nötväcka	*Sitta europea*	2				3	3	4	3	9	4	2	5	6	6	10	60
Eurasian Treecreeper	trädkrypare	*Certhia familiaris*										1		2		1		7
Mistle Thrush	dubbeltrast	*Turdus viscivorus*														1		2
Fieldfare	björktrast	*Turdus pilaris*			4	1		18	1		7	1		7		2	25	127
Redwing	rödvingetrast	*Turdus iliacus*			5											1		9
Common Blackbird	koltrast	*Turdus merula*							1					1				2
Eurasian Blackcap	svarthätta	*Sylvia atricapilla*																1
Goldcrest	kungsfågel	*Regulus regulus*						5				2				2		14
Bohemian waxwing	sidensvans	*Bombycilla garrulus*			4	25		42		11		2		83		9	128	1,078
Hawfinch	stenknäck	*Coccothraustes coccothraustes*																2
Eurasian Siskin	grönsiska	*Carduelis spinus*												1	1			4
Eurasian Bullfinch	domherre	*Pyrrhula pyrrhula*	134	34	93	108	121	144	132	99	88	229	207	250	162	146	329	3,416
Pine Grosbeak	tallbit	*Pinicola enucleator*	22											3			1	96
Red / Parrot Crossbill	mindre / större korsnäbb	*Loxia curvirostrata / pytopsittacus*		102	2	62		2		92		2			19			573
Two-barred Crossbill	bändelkorsnäbb	*Loxia leucoptera*								5								8
Common chaffinch	bofink	*Fringilla coelebs*				1	2				1			1		1		6
Brambling	bergfink	*Fringilla montifringilla*		1												1	1	3
Total	**totalt**		505	513	436	678	536	566	552	706	527	725	681	811	559	560	844	**15,907**

Appendix 2. Full correlations between bird and forest variables

	r_s, significance					
Forest variable *Skogsvariabel*	N forest species *Antal skogsarter*		N ind, forest species *Antal ind, skogsarter*		N ind, forest specialists *Antal ind, skogsspecialister*	
Open ground, area *Öppen mark, yta*	–0.45	**	–0.80	**	–0.60	**
Young forest (0–30 years), area *Ung skog (0–30 år), yta*	–0.20	NS	–0.42	*	–0.11	NS
Middle-aged forest (30–70 years), area *Medelålders skog (30–70 år), yta*	0.46	**	0.75	***	0.54	**
Forest ready for cutting (>70 years), area *Avverkningsmogen skog (>70 år), yta*	–0.34	*	–0.67	***	–0.53	**
Fully grown forest (middle-aged + ready for cutting; >30 years), area *Fullt uppvuxen skog (medelålders + avverkningsmogen; >30 år), yta*	0.31	(*)	0.23	NS	0.15	NS
Old forest (>140 years), area *Gammal skog (>140 år), yta*	0.39	*	0.38	(*)	0.21	NS
Older forest, rich in deciduous trees (>80 years), area *Äldre lövträdsrik skog (>80 år), yta*	–0.37	(*)	–0.73	***	–0.47	*
Standing volume of wood in middle-aged forest *Stående skogsvolym i medelålders skog*	0.43	*	0.71	***	0.50	**
Standing volume of wood in forest ready for cutting *Stående skogsvolym i avverknoingsmogen skog*	0.37	*	0.72	***	0.53	**
Standing volume of wood in fully grown forest *Stående skogsvolym i fullt uppvuxen skog*	0.40	*	0.76	***	0.52	**
Dead wood, volume *Död ved, volym*	0.39	*	0.65	***	0.39	*

Appendix 3. Full correlations between bird and weather variables

	r_s, significance					
Weather variable *Vädervariabel*	N forest species *Antal skogsarter*		N ind, forest species *Antal ind, skogsarter*		N ind, forest specialists *Antal ind, skogsspecialister*	
Annual temperature (April–March) *Årstemperatur (april–mars)*	0.18	NS	0.08	NS	0.22	NS
Winter temperature (November–March) *Vintertemperatur (november–mars)*	0.07	NS	–0.01	NS	0.07	NS
Summer temperature (April–August) *Sommartemperatur (april–augusti)*	0.24	NS	0.17	NS	0.47	**
Annual precipitation (April–March) *Årsnederbörd (april–mars)*	–0.27	NS	–0.21	NS	0.10	NS
Winter precipitation (November–March) *Vinternederbörd (november–mars)*	–0.36	*	–0.30	(*)	–0.10	NS
Summer precipitation (April–August) *Sommarnederbörd (april–augusti)*	–0.20	NS	–0.23	NS	–0.10	NS