

How generalist are these forest specialists? What Sweden's avian indicators indicate

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Abstract

Monitoring of forest biodiversity and habitats is an important part of forest conservation, but due to the impossible task of monitoring all species, indicator species are frequently used. However, reliance on an incorrect indicator of valuable habitat can reduce the efficiency of conservation efforts. Birds are often used as indicators as they are charismatic, relatively easy to survey, and because we often have knowledge of their habitat and resource requirements. In the Swedish government's environmental quality goals, there are a number of bird species identified as being associated with 'older' and 'high natural value' forests. Here we evaluate the occurrence of four of these indicator species using data from 91 production forest stands and 10 forest reserves in southern Sweden. The bird species assessed are willow tit *Poecile montanus*, coal tit *Periparus ater*, European crested tit *Lophophanes cristatus* and Eurasian treecreeper *Certhia familiaris*. For the production stands assessed, these indicator species exhibited no significant preferences regarding forest composition and structure, indicating a wider range of habitat associations than expected. These species frequently showed territorial behavior in forest stands <60 and even 40 years of age; much younger than the 120-year threshold for 'older forest' as defined by governmental environmental goals. As almost 80% of the production stands ≥ 10 years old included at least one of the four indicator species, this raises questions regarding the suitability of these species as indicators of forests of high conservational value in southern Sweden. Notably, besides the four species assessed here, none of the additional indicator taxa identified by the government, were recorded in the 10 reserves. This outcome may reflect the difficulties involved in finding bird indicator species indicative of high natural values in this region. Our results highlight the importance of coupling bird surveys with quantified assessments of proximate vegetation cover.

Introduction

The rate of human-induced global ecological change during the past 50 years is unprecedented, and our actions threaten more species with extinction now than ever before (Diaz *et al.*, 2019). Conserving sufficient amounts of the world's varied forest ecosystems is critical to countering species loss, due to the unique biodiversity these systems provide (Lindenmayer & Franklin, 2002; Brockerhoff *et al.*, 2017). Monitoring of forest biodiversity and habitats is an important part of forest conservation, but due to the impossible task of monitoring all species in a habitat, indicator species are frequently used instead – by public organizations (Andersson, Andersson & Eriksson, 2018), forest companies (Ekenstedt & Olsson-Cipi, 2008), as well as in research (Williams & Ellis, 2018). An indicator species can be defined as '...an organism whose characteristics (e.g. presence or absence,

population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient or expensive to measure for other species or environmental conditions of interest' (Landres, Verner & Thomas, 1988). The use of indicator species has, however, been questioned over the years, and the main critiques stem from the fact that the link between the species and the hypothesized biological value of particular habitat is rarely tested (Lindenmayer & Likens, 2011). For example, the connection between the species and the environment in which it occurs may be insufficiently documented, or that insufficient studies have been conducted in environments where the species is presumed not to occur (Versluijs, Hjältén & Roberge, 2019). Reliance on an incorrect indicator of high biodiversity or otherwise valuable habitat can be negative for at least two reasons. First, habitats can be falsely designated as valuable for biodiversity; thereby reducing the efficiency of conservation efforts, or

causing conservation targets to be erroneously considered as being achieved. Second, such mistakes can reduce the confidence of the public, managers and policy makers in the use of indicators, with negative implications for species conservation efforts in general.

Birds are often used as indicators as they are charismatic, relatively easy to survey, and one of the species groups for which we have the most knowledge regarding habitat and resource requirements. For example, the occurrence of woodpeckers has been used to indicate a high diversity of forests birds in general (Mikusinski, Gromadzki & Chylarecki, 2001; Drever *et al.*, 2008), whereas the Eurasian treecreeper is often used to indicate the presence of old forests, and by association, biologically valuable forests (Suorsa *et al.*, 2005; Solonen & Jokimaki, 2011). In the Swedish government's environmental quality goals (sverigesmiljomal.se), there are a number of bird species identified as indicating different categories of high conservation value forest (Table 1). Some species encountered during the systematically surveyed routes of the Swedish Bird Survey (SBS) are used to indicate 'high natural values in forest', whereas others are used to indicate 'older forest', defined as over 120 years of age in southern Sweden (Ram *et al.*, 2017). The choice of which bird species to use as an indicator is based on studies of their habitat associations in northern Europe (Jansson, 1998; Mikusinski *et al.*, 2001; Ottvall, Green & Lindström, 2006; Roberge & Angelstam, 2006; Summers, 2007), with additional requirements that they are common enough to be useful for evaluating population trends. In this regard, the population trends in these species is currently being used to support claims by governmental organizations regarding the situation for forests biodiversity in general, and for evaluating conservation actions in production forests (Ram *et al.*, 2017; Andersson *et al.*, 2019). It is therefore vital that the bird species used to justify such conclusions accurately reflect the availability of valued categories of forest habitat.

Here we evaluate the habitat associations of four of these indicator species using a large pool of standardized survey data from 10 reserves and 91 production stands in southern Sweden (Table 2). The latter represent a variety of production forest types in terms of age, proportion of deciduous trees and geographical distribution, though the majority consists of intensively managed even-aged Norway spruce *Picea abies* or Scots pine *Pinus sylvestris* dominated stands. The bird species assessed were willow tit *Poecile montanus*, coal tit *Periparus ater*, European crested tit *Lophophanes cristatus* and Eurasian treecreeper *Certhia familiaris*. These species were assessed because each is used as an indicator of both 'high natural value' and 'older forests' (Table 1), and they occur in the survey region. We evaluated the occurrence of these four indicator bird species in relation to several forest attributes, including tree age, tree species composition and structural diversity. We were specifically interested in determining (1) to what extent these birds indicate 'high natural values' and/or 'older forest' conditions in southern Sweden; and (2) how the occurrence of these species relates to stand variables including tree age and tree species composition. We place our results within the larger context of using

Table 1 Indicators for 'high natural values in forest' and/or 'older forests' according to the Swedish government's environmental quality goals (sverigesmiljomal.se). The four first (most common) are the indicator species evaluated in this study. The population sizes (breeding pairs) is from the region of the study, that is, the counties of Västra Götaland, Jönköping, Kronoberg, Halland, and Kalmar (Ottosson *et al.*, 2012)

	High natural values in forest	Older forest	Population size
Eurasian Treecreeper <i>Certhia familiaris</i>	X	X	270 000
Coal tit <i>Periparus ater</i>	X	X	167.000
European crested tit <i>Lophophanes cristatus</i>	X	X	104.000
Willow tit <i>Poecile montanus</i>	X	X	77.000
March tit <i>Poecile palustris</i>	X		72.500
Eurasian bullfinch <i>Pyrrhula pyrrhula</i>	X	X	46.500
Long-tailed tit <i>Aegithalos caudatus</i>	X		13.200
Western capercaillie <i>Tetrao urogallus</i>	X	X	13.100
European Green Woodpecker <i>Picus viridis</i>	X		7900
Spotted nutcracker <i>Nucifraga caryocatactes</i>	X		5650
Hazel grouse <i>Tetrastes bonasia</i>	X		5335
Stock dove <i>Columba oenas</i>	X		2810
Lesser spotted woodpecker <i>Dryobates minor</i>	X		2020
Siberian tit <i>Poecile cinctus</i>	X	X	0
Siberian jay <i>Perisoreus infaustus</i>	X	X	0
Eurasian Three-toed Woodpecker <i>Picoides tridactylus</i>		X	0

Ottosson *et al.* (2012) Fåglarna i Sverige – antal och förekomst. SOF, Halmstad.

indicator species for finding stands of high conservational value, and as a means of evaluating the effectiveness of efforts to improve the quality of habitat provided by production forests.

Materials and methods

Study area and stands included

All surveys were conducted in the region Götaland in the hemi-boreal zone of southern Sweden (Ahti, Hamet-Ahti & Jalas, 1968). The mean temperature (1961–1990) in the area is approximately -3°C in January, and 16°C in July, and the precipitation is 400–600 mm year⁻¹. Forests cover 63% of the land area in the region. The landscapes of southern Sweden have undergone a dramatic change the last 100–400 years. From domination by traditional cultural landscapes with open and grazed forests of mixed tree species, the region is today largely covered by dense conifer-

Table 2 Publications included in the study and stand characteristics

	Year surveyed	No stands	Age	Tree species (% refers to basal area) and stand description
Lindbladh <i>et al.</i> (2014b)	2013	13	~4–8	Early rotation Norway Spruce plantations with high proportions of naturally regenerated Birch and other broadleaves
Lindbladh <i>et al.</i> (2017)	2016	8	10–90	Norway Spruce 77–100%
Lindbladh <i>et al.</i> (2019)	2017	50	52–59	10 ≥ 94% Pine
			75–87	10 ≥ 82% Pine
			50–56	10 ≥ 85% Spruce
			75–85	10 ≥ 82% Spruce
			100+	10 reserves ≥ 85% conifers
A. Felton, P.-O. Hedwall, E. Holmström, R. Trubins, J. Lagerstedt, and M. Lindbladh (in prep)	2018	30	24–59	19 Spruce dominated (>50%) 11 Birch dominated (>50%)

dominated managed forest stands (Lindbladh *et al.*, 2011). This borealization process is the result of a combination of anthropogenic (the agricultural revolution, forest grazing, silviculture, etc.) and natural (climate, species immigration, etc.) drivers (Lindbladh *et al.*, 2014a). Industrial silviculture was intensified in the 1950s and today production forestry dominates. Only ~2% of the productive forest land (timber production capacity >1 m³ ha⁻¹ year⁻¹) in southern Sweden is formally protected (table 1.5 in Nilsson *et al.*, 2019). This enables Sweden with just 1% of the world's productive forest land to be the third largest exporter of pulp, paper and sawn timber (SFIF, 2018). Norway spruce dominates (47%) standing volume in the study region, closely followed by Scots pine (30%) (Nilsson *et al.*, 2019). The majority of production forests in Sweden are certified by voluntary certification schemes (i.e. FSC or PEFC), requiring that individual trees or groups of trees of higher conservation value are excluded from harvesting at clear felling (Johansson *et al.*, 2013), as well as the retention of certain categories of dead trees, the use of buffer zones and the protection of sensitive habitats (FSC, 2010). One recent estimate is that retained patches of forest represent 11% of harvested areas 1 year after final felling (Skogsstyrelsen, 2019).

Conifer dominated production forests are generally planted with improved plant material in even-aged stands after soil scarification. These stands are pre-commercially and commercially thinned two to three times during a rotation. The main purpose of the pre-commercial thinning is to remove any undesired excess of naturally regenerated broadleaves, mainly birch *Betula pendula/pubescens*. Stands are clear-cut after a rotation period of between 45–70 and 60–100 for Norway spruce and Scots pine, respectively, depending, for example, on site conditions. Under natural conditions individuals of both tree species can regularly live at least 200–300 years (Kuuluvainen *et al.*, 2002). Birch is the third most common tree (11%) in the region. Birch dominated commercial stands are mostly naturally regenerated (Rytter *et al.*, 2014) and are final cut at around the age of 50, and their maximum age under natural conditions is estimated to be around 200 years (Hofgaard, 1993). Less common trees in the region are oak spp. *Quercus robur/petraea* (3.3%), aspen

Populus tremula (2.6%), alder *Alnus glutinosa* (2.4%) and beech *Fagus sylvatica* (1.6%) (Nilsson *et al.*, 2019).

We used survey data from three published (Lindbladh *et al.*, 2014b, 2017, 2019) and one unpublished study (A. Felton, P.-O. Hedwall, E. Holmström, R. Trubins, J. Lagerstedt, & M. Lindbladh, in prep). The 101 stands included in the study were distributed in the forest-dominated counties of Halland, Kronoberg, Kalmar, Jönköping and Västra Götaland (Table 2). The 91 production stands used were chosen due to survey requirements, see previous publications for more information (Lindbladh *et al.*, 2014b, 2017, 2019). For most part they were typical of conifer-dominated planted production forests in the hemi-boreal vegetation zone of Sweden. The only exceptions were the birch dominated production stands, and Norway spruce production stands in excess of 80 years of age. Stand ages spanned from newly regenerated stands of around 5 years since establishment, to 90 years and well in excess of standard final cutting age. All forest reserves were conifer dominated. Like all forests in southern Sweden, they have a history of human land use in some form, such as forest grazing or selective cutting, but with all or parts of the reserves naturally regenerated (sometimes post fire), and containing a number of older trees. It was not possible to core the trees, but according to management plans, the reserves harbored a large number of trees over 100 years of age, in many cases >120 years, and occasionally up to 250 years of age. Based on the reserves' management plans and maps, survey plots were randomly placed in areas possessing the oldest parts of the reserves.

Bird surveys

All stands had a minimum size of 4 ha to reduce the risk of including birds associated with the stand's border zone. All surveys were done using the point count survey method (Bibby, Burgess & Hill, 2000). We used a survey radius of 30 m (A. Felton, P.-O. Hedwall, E. Holmström, R. Trubins, J. Lagerstedt, & M. Lindbladh, in prep) or 40 m (all other stands) as this threshold distance limits the birds assessed to only those located within the stand, and reduces the risk of double counting birds at two survey points.

Furthermore, these radii are less than the maximum distance observers are estimated to be able to differentiate the distance to calling birds (i.e. 65 m, see Allredge, Simons & Pollock, 2007). Four survey points were located within each stand, with the proviso that the distance between two survey points was >60 or >80 m (depending on the study), and >50 m from the stand edge. We surveyed each of the stands four times; twice in early spring (late March/early April) and twice in late spring (mid-late May).

All point count surveys were conducted by ornithologists (AF, ML and Thomas Nyberg) experienced with both bird identification and point count surveys, which is important for high quality bird data collection (Farmer, Leonard & Horn, 2012). Most identification was made acoustically rather than visually. In cases of uncertainty with respect to the number of individual birds calling, the most conservative estimate of abundance was used. All birds encountered were noted, but only individuals performing territorial behaviour (song in almost all cases) were included in the data analyses. The survey results from the four points in each stand were lumped, hence the stand is treated as one observation. As an estimate of the abundance of each bird species in a given stand (based on the four survey points combined in each stand), we used the highest value attained from the four separate surveys conducted in each stand (Toms *et al.*, 2006).

For more information on the bird survey methodology see Lindbladh *et al.* (2019)

Stand level structures

A similar methodology for surveying stand level forest structures was used across all studies. Ten plots in each stand were surveyed for living trees, living shrubs and dead wood (Table 3). Four of the plots were the same as the plots in the bird inventory, see above. The remaining six were randomly distributed 30 m from the bird plots. The DBH (diameter at breast height) was measured, and basal area calculated, for all living woody species >1.3 m tall within a

radius of 10 m from the center of the plot; in a few cases 7 or 15 m from the center depending on whether the stand was unusually dense, open or heterogeneous. To assess structural complexity, the coefficient of the variation in tree sizes (DBH) was calculated as the ratio of the standard deviation to the mean. Shannon's diversity based on the basal area distribution between tree species was used as an indicator of tree species diversity.

Statistics

We used generalized linear models (GLM) to estimate the effects of stand characteristics on the four bird species occurrences. Due to collinearities among the explanatory variables we analysed the seven variables (stand age, tree species richness, Shannon diversity of tree species, total basal area, percentage Scots pine, percentage deciduous tree species and tree size variation) in separate models and corrected the P-values for multiple comparisons by the false discovery rate correction (Benjamini & Hochberg, 1995). All species occurred in low numbers and we therefore chose to model the presence-absence with a binomial error distribution and cloglog-link. As survey radius differed between the stands (30 or 40 m) the log-transformed surveyed area was included as an offset variable in all GLMs. As none of the bird species of interest occurred in stands <10 years, these stands were excluded from the GLM. All other stands were included, that is, the 78 production stands and the 10 reserves. Additionally, we also performed an Indicator Species Analyses (ISA) to detect if some of the four individual species or combinations of these species are indicators of different age categories [0–19, 20–39, 40–59, 60–89, reserves (90+) years]. The ISAs were done with 999 permutations. All analyses were done in R version 3.4.1 (R Core Team, 2019). The GLMs were done in the stats package, whereas the ISA was done by applying the indicpecies package (De Caceres & Legendre, 2009).

Ecology and status of the four indicator species

Willow tit *Poecile montanus*

Willow tits breed principally in conifer forest in northern Europe (Gosler, Clement & Garcia, 2019). Around 800 000 pairs breed in Sweden (~20th most common species), in conifer and mixed conifer-broadleaf forest throughout most of the country, but with a predominance in areas with *Pinus* dominated forests (Ottosson *et al.*, 2012). Willow tit is mainly a resident species, but northern populations are dispersive and occasionally eruptive, resulting in unusually high population densities both within and often outside its normal range. Although the Swedish population as a whole, however, has been stable during the last two decades (Green, Haas & Lindström, 2019), their numbers have increased in the study region during this period (Lindbladh *et al.*, 2017). The adult diet during summer is divided almost equally between plant and animal food, with the diet of nestlings

Table 3 Stand structures for reserves ($n = 10$), production stands >10 years ($n = 78$) and <10 years ($n = 13$)

	Stand type					
	Reserves		10–90 years		<10 years	
	Mean	SD	Mean	SD	Mean	SD
No tree species	4.9	1.8	3.9	1.7	4.3	1.3
Total basal area ha ⁻¹	24.25	3.68	25.50	9.29	3.01	5.41
Share broadleaves basal area	0.07	0.08	0.15	0.26	0.74	0.24
Share scots pine basal area	0.59	0.16	0.27	0.41	0.01	0.01
Mean diameter at breast height	13.23	2.93	17.65	4.59	1.90	2.33
Variation tree size	0.88	0.21	0.51	0.26	0.54	0.23
Shannon tree species diversity	0.82	0.22	0.38	0.32	0.55	0.21

reflecting that of the adults (Gosler *et al.*, 2019). Nests are placed in holes or crevices up to three meters from the ground in rotting tree trunks or old stumps, excavated by itself or by other species, for example, woodpeckers. Territory size varies according to habitat, but generally ranges from 5 to 15 ha (Gosler *et al.*, 2019). Some studies have concluded that this species prefers old forests (Solonen & Jokimaki, 2011; Cirule *et al.*, 2017; Gosler *et al.*, 2019), whereas other studies have failed to find such a preference (Virkkala *et al.*, 1994). Additional studies have found that willow tit prefer structurally complex forests (Eggers & Low, 2014) with standing decaying deciduous trees (Vatka *et al.*, 2014), especially in damp habitats (Lewis *et al.*, 2007).

Coal tit *Periparus ater*

Coal tits breed conifer forests, primarily in *Picea* dominated stands, but also in mixed forest often dominated by *Betula* and *Pinus* (Gosler & Clement, 2019a). Although it is a non-migratory resident species, it does make short-distance altitudinal distributional shifts. About 410 000 pairs breed throughout Sweden, excluded only from the northernmost parts of the country, and primarily occur in conifer (most common in *Picea*) and mixed forests (Ottosson *et al.*, 2012). For the last two decades the overall population trend in Sweden is stable, as is the case for the study region (Lindbladh *et al.*, 2017; Green *et al.*, 2019). During summer coal tits feed on adult and larval bugs, as well as *Picea* seeds (Gosler & Clement, 2019a). The diet of nestlings is similar but with fewer seeds. Nests are placed in hollows or the cavities of tree trunks or old stumps, and include the abandoned holes of rodents and woodpeckers (Gosler & Clement, 2019a). Their territory size is not well studied but is likely to be small, with a radius of approximately 100 m (~3 ha) in good habitat. Studies of stand structure preferences are relatively scarce, but one study in Scotland indicates that coal tit avoids forests with large variation in canopy cover (Calladine *et al.*, 2017).

European crested tit *Lophophanes cristatus*

Crested tits breed in northern Europe in stands of *Pinus* and *Picea*, as well as in conifers in mixed woodlands (Gosler & Clement, 2019b). It is primarily a resident species, but nomadic in winter. Around 400 000 pairs breed in conifer dominated forests and mixed forests throughout Sweden (Ottosson *et al.*, 2012). The population trend is increasing in Sweden on the whole over the last two decades (Green *et al.*, 2019), but its populations are stable in the study region during the same time period (Lindbladh *et al.*, 2017). Their food during the breeding season mostly consists of small invertebrate adults and larvae, whereas nestling diet consists principally of spiders and some *Pinus* seeds (Gosler & Clement, 2019b). Nests are placed mostly within 3 m of the ground in the holes of dead or decaying tree trunks, branches or stumps and occasionally in living trees. Territory size is not well known, but their home range (most of which

is territory) is 6–11 ha in most of Europe. Studies in Finland and Scotland have found that the species is most abundant in old-growth forests (Virkkala *et al.*, 1994; Summers *et al.*, 1999; Calladine *et al.*, 2017). In some regions it is more common in areas with greater diversity of tree heights, but has a negative association with increased variation in forest density, and with stands with an understory of regenerating trees (Calladine *et al.*, 2017).

Eurasian treecreeper *Certhia familiaris*

Eurasian treecreepers breed in forests and woodlands. According to Harrap (2019) this species generally requires large mature trees with many bark cracks and crevices, for foraging, roosting and nesting. It tends to favor older stands of *Picea*, but their habitat preferences are complex. 750 000 pairs breed through most of Sweden (Ottosson *et al.*, 2012). The population has increased in Sweden as a whole over the last two decades (Green *et al.*, 2019), but their population size is stable in the study region over the same time period (Lindbladh *et al.*, 2017). Eurasian treecreepers feed on insects and spiders during summer, and also consume *Pinus* and *Picea* seeds during winter (Harrap, 2019). Their nests are placed up to 16 m above ground behind a flap of loose bark or in a crevice on a tree trunk (Harrap, 2019). The radii from 30 to 200 m from the nest is the most important spatial scale for forest patch occupancy by the species (Suorsa *et al.*, 2005), which broadly spans the territory size of 10 ha suggested by Kuitunen & Törmälä (1983). A large number of Finnish studies have shown that this species prefers old and large trees in both managed stands and in old-growth forests (Virkkala *et al.*, 1994; Kouki & Vaananen, 2000; Suorsa *et al.*, 2005; Jokimaki & Solonen, 2011).

Results

None of the four indicator species assessed occurred in stands <10 years old, and except for the ISA only results from the 78 production stands ≥10 years and the 10 reserves are presented. Overall, the four indicators were between the 6th and 13th most common species in terms of abundance in the 78 production stands; treecreeper had the highest abundance and crested tit had the lowest of the indicators (Fig. 1). In the reserves the indicators had between the 3rd and 16th highest abundance of all bird species; treecreeper having the highest abundance, and coal tit having the lowest, of the indicators (Fig. 2). After excluding the 10 reserves and the stands <10 years old, they were encountered in 37% (willow tit), 38% (coal tit), 31% (crested tit) and 44% (treecreeper) of the stands (Fig. 3; Table 4). In total 61 (78%) of the production stands harbored at least one indicator species, whereas all reserves harbored at least one of the indicator species. The youngest stands with crested tit were 38 years of age, whereas the other four species were recorded in stands ≥23 years old. Willow tit and coal tit were recorded in four and two, respectively, of the 10 reserves, whereas the other three species were found in seven of the 10 reserves (Fig. 3; Table 4).

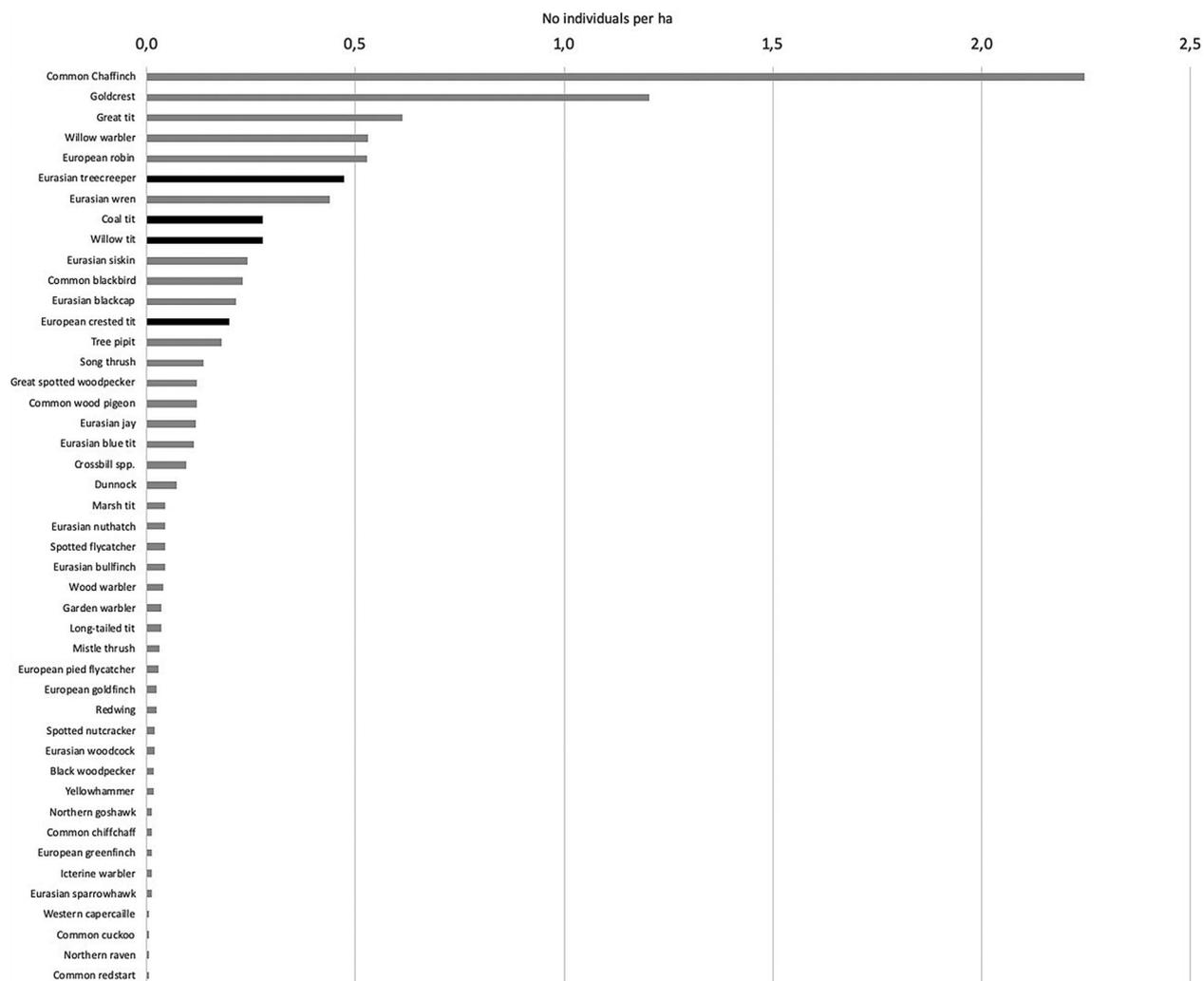


Figure 1 Average number of individuals per hectare in production stands >10 years old ($n = 78$).

Coal tit was positively associated with the total basal area of the forest, whereas negatively associated with the percentage of Scots pine according to the GLMs (Table 5). There were no statistically significant effects of any variables on the occurrence of the other three bird species. None of the individual species were a significant indicator species according to the ISA for an individual age category but coal tit, treecreeper and willow tit individually indicated the four oldest age categories (20+) together (Table 6). The indicator value (IV; ranging from 0 to 1 with one indicating that the species occurs in all stands of the group and nowhere else) ranged between 0.606 and 0.686 ($P = 0.002$ – 0.016) for these species. Additionally, crested tit individually ($IV = 0.635$, $P = 0.003$), as well as coal tit and crested tit together ($IV = 0.433$, $P = 0.050$) indicated the summed three oldest (40+) age classes. Crested tit and treecreeper together indicated the oldest (60+) two age classes ($IV = 0.550$, $P = 0.003$), whereas the only significant indicator of the oldest age category (90+, reserves) was the common presence of crested tit, treecreeper and willow tit ($IV = 0.444$, $P = 0.021$).

Discussion

Our study highlights the importance of conducting bird surveys in combination with assessments of the vegetation cover, and the results raise a number of questions regarding the true habitat requirements of the four indicator species with respect to their association with ‘older’ and ‘high natural value’ forests. In terms of occurrence, the four indicators were not uncommon in the production stands as they were encountered in 31–44% of the 78 stands. The occurrence rates for the conifer specialists coal tit and crested tit is even higher if only stands with >50% conifers were included; 43 and 34%, respectively. Moreover, as only a subset (~1.2–2 ha) of each stand was surveyed, these results are conservative with respect to the true occurrence of these species in these production forests.

Regarding forest age, none of the four species had a preference for old stands (Table 5). All species were regularly found exhibiting territorial behavior in stands that were under 60 of age, and except crested tit, even in

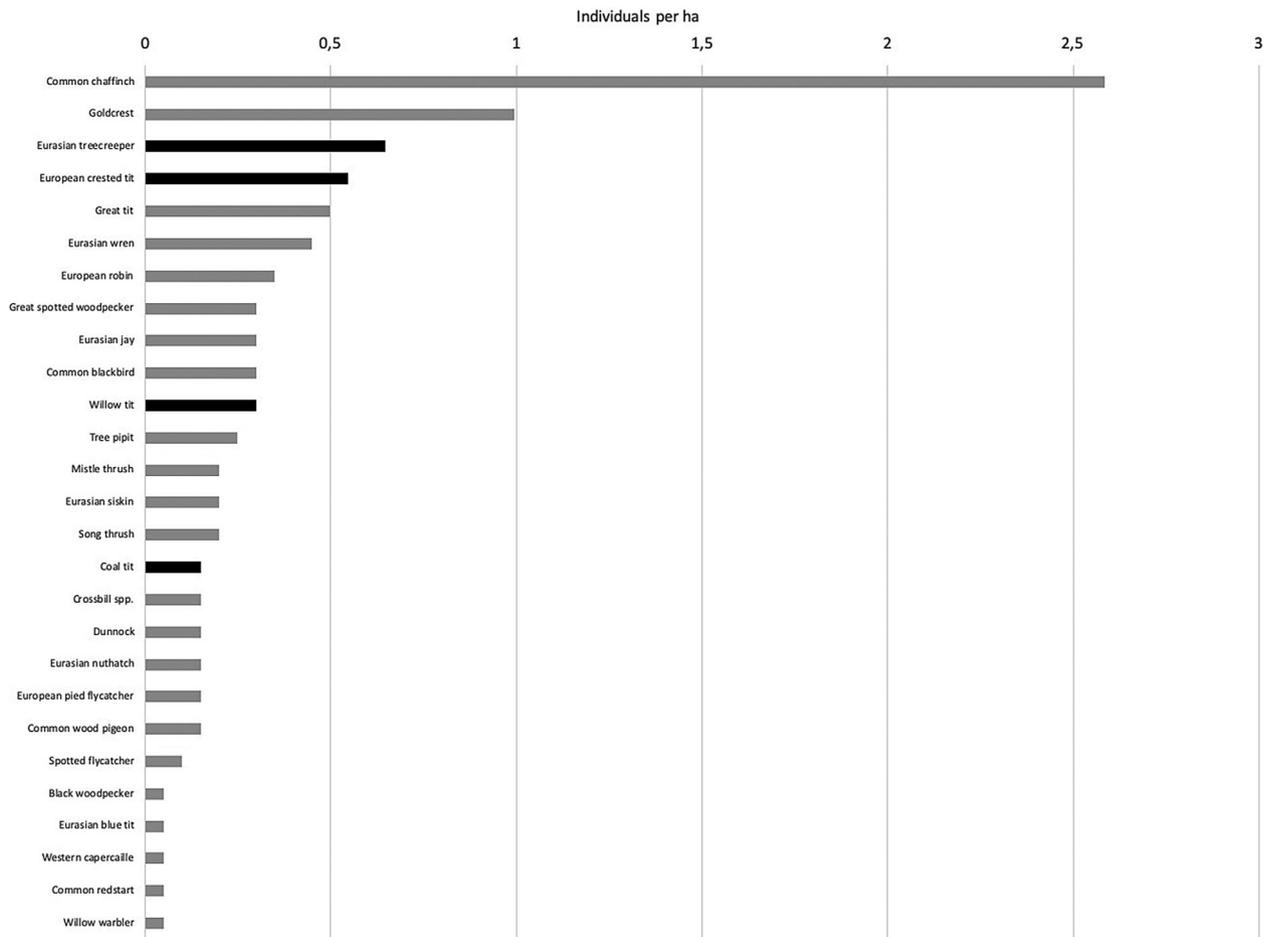


Figure 2 Average number of individuals per hectare in the reserves ($n = 10$).

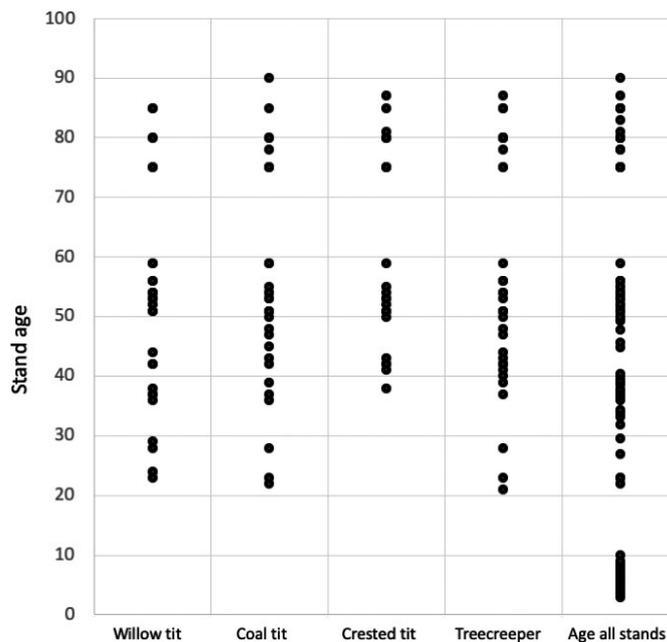


Figure 3 Stand ages where, respectively, species showing territorial behaviour occurred. All production stands included but not the reserves.

Table 4 Number and percentage of stands with occurrence of individual performing territorial behaviour. Only production stands ≥ 10 years ($n = 78$) or reserves ($n = 10$) are included

	Number of production stands ($n = 78$)	Stand age range	No stands < 40 year		No stands < 60 year		No stands $\geq 30\%$ broadleaves	% of reserves ($n = 10$)
Willow tit	29 (37%)	23–85	8 (10%)	23 (29%)	5 (6%)	40		
Coal tit	30 (38%)	22–90	6 (8%)	22 (28%)	1 (1%)	20		
Crested tit	24 (31%)	38–87	1 (1%)	15 (19%)	2 (3%)	70		
Treecreeper	34 (44%)	21–87	5 (6%)	24 (31%)	6 (8%)	70		

Table 5 The generalized linear models estimation of the effects of stand characteristics on the four bird species occurrences

Bird species	Variable	Coefficient	<i>P</i> (adjusted)
Coal tit	Stand age	-0.013	0.302
	No of tree species	0.132	0.353
	Shannon tree species diversity	-0.338	0.695
	Variation tree size	-1.216	0.302
	Total basal area	0.085	0.007
	% deciduous trees	-0.362	0.781
Crested tit	% Scots pine trees	-2.349	0.013
	Stand age	0.018	0.163
	No of tree species	0.079	0.569
	Shannon tree species diversity	0.814	0.302
	Variation tree size	0.596	0.476
	Total basal area	-0.035	0.302
Treecreeper	% deciduous trees	-1.636	0.388
	% Scots pine trees	0.915	0.196
	Stand age	0.003	0.758
	No of tree species	0.131	0.322
	Shannon tree species diversity	0.935	0.222
	Variation tree size	-0.004	0.994
Willow tit	Total basal area	0.036	0.222
	% deciduous trees	1.527	0.084
	% Scots pine trees	-1.082	0.133
	Stand age	-0.01	0.396
	No of tree species	0.132	0.353
	Shannon tree species diversity	0.43	0.569
Treecreeper	Variation tree size	-0.134	0.877
	Total basal area	0.037	0.222
	% deciduous trees	0.722	0.489
	% Scots pine trees	-0.851	0.302

stands <40 years of age (Fig. 3; Table 4). This is much younger than the 120-year threshold for 'older forest' defined in the government's environmental goals (sverigesmiljomal.se). The government's assessment of developments in the availability of valuable forest habitat is based on the presence of the 16 indicator species during the SBS's annual inventories from 716 routes across the country (Green *et al.*, 2019). In the assessment, all of the 16 indicators are treated equally. This means that the individual population trends of each of the four common indicator species in this study have the same influence on outcomes and their interpretation as the rarer species. Because of this conclusion, stemming from such

Table 6 Results from the species indicator analysis. The age categories are 0–19, 20–39, 40–59, 60–89 and reserves (90+) years

Stand age categories	No of age categories	Indicator species	Indicator value	<i>P</i> -value
20+	4	Treecreeper	0.686	0.002
20+	4	Coal tit	0.606	0.014
20+	4	Willow tit	0.616	0.016
40+	3	Crested tit	0.635	0.003
40+	3	Crested tit & coal tit	0.433	0.050
60+	2	Crested tit & treecreeper	0.550	0.003
Reserves	1	Crested tit, treecreeper & willow tit	0.444	0.021

assessments may not be reliable, if used to infer changes in the availability of valuable forest habitat.

None of the four species were significant indicators of an individual stand age category (Table 6). However, in practical conservation indicator species are typically designed to be used in combination. The indicator test showed that crested tit in combination with treecreeper do indicate the oldest production stand age category (60–89 years). Although interesting, this result is probably of limited value, as this age range does not represent an old forest from a biological or conservation perspective. Of more interest is that if these two species occur together with willow tit, this seems to indicate the older reserves in our study. This result may prove useful during the selection of reserves or set-asides.

The four indicator species are also suggested to indicate high natural values, values that were not common in most of the 74 production stands according to our stand structure inventory (Table 3). In addition, the four indicators do not seem to have a preference for the stands that actually had a higher availability of structures known to be important for forests biodiversity, for example, tree species diversity or variation in tree sizes (Lindenmayer & Franklin, 2002) (Table 5). Even if the four birds apparently do not require old-growth forests, it is somewhat surprising that they were not associated with any of these structures, and that many individuals included as part of their territory intensively managed production stands; an environment often considered to be depauperate habitat for these supposed habitat specialists (Nilsson, 1979; Rosenvald *et al.*, 2011; Eggers & Low, 2014).

Although there are many factors in the environment that affect a species choice of breeding habitat, the availability of suitable nesting substrate is essential (Vatka *et al.*, 2014). According to del Hoyo *et al.* (2017) the three tit species assessed in our study prefer to nest in holes in dead or decaying tree trunks. In a study of crested tit in a native *Pinus* forest in Scotland, almost all (33 of 36) nests were located in dead trees or stumps (Denny & Summers, 1996), and a study by Vatka *et al.* (2014) showed the importance of standing decaying trees as nest sites for willow tit. Our study may indicate that these species have less narrow nesting habitat preferences than indicated in the literature. Perhaps these species are able to use the stumps provided after clear-cutting or thinning (common in Swedish production forests), or the snags (high-stumps) that are created according to certification requirements (Gustafsson & Perhans, 2010). Unfortunately, not all the stands included in our study were surveyed for dead wood, and as such the availability of these structures were not included in the analyses. Nevertheless, for those stands in which dead wood was surveyed, only low volumes of these structures were found. In the 40 production stands assessed in Lindbladh *et al.* (2019), the average total dead wood volume was $4.9 \text{ m}^3 \text{ ha}^{-1}$, of which only $1.4 \text{ m}^3 \text{ ha}^{-1}$ consisted of standing dead wood: For A. Felton, P.-O. Hedwall, E. Holmström, R. Trubins, J. Lagerstedt, and M. Lindbladh (in prep), the average volume of dead wood was $3.2 \text{ m}^3 \text{ ha}^{-1}$. These values are far lower than in Europe's natural forests (Müller & Büttler, 2010), and even lower than southern Sweden's averages of $7.5 \text{ m}^3 \text{ ha}^{-1}$ ($3.4 \text{ m}^3 \text{ ha}^{-1}$ standing dead) found in non-formally protected productive forest lands (Jonsson *et al.*, 2016). This indicates that large volumes of dead wood may not be crucial determinants of breeding habitat by these bird species.

Altogether, the result may tentatively be used to infer that the four indicator species, perhaps except crested tit, have broader habitat associations than was understood at the time they were chosen to be indicators of older and higher natural value forests. Our results are therefore consistent with at least some other studies that have concluded that three of these species do not require old-growth forests as habitat, namely crested tit (Summers, 2007), willow tit (Virkkala *et al.*, 1994; Vatka *et al.*, 2014) and coal tit (Patterson, Ollason & Doyle, 1995).

We have in detail only analyzed the four most common of the 16 indicators according to the government's environmental assessment. Of the additional indicator species in the region (Table 1); march tit *Poecile palustris* and bullfinch *Pyrrhula pyrrhula* were found in four stands each in our study, and long-tailed tit *Aegithalos caudatus* was recorded in two. Although our results do not confirm the suitability of these three species as indicators, their rarity within intensively managed production stands is more consistent with their status as indicators of old and high value natural forests. Notably, none of these three species, nor any of the additional indicator species (Table 1), were recorded in the 10 reserves (Fig. 2). This may reflect the fact that several of the reserves included in this study lacked some old-growth

forest characteristics (see Lindbladh *et al.*, 2019). However, the outcome may also reflect the difficulties involved in finding bird species indicative of high natural values in this region. The resultant circumstances are one in which relatively abundant indicator species are being used which occur from intensively managed production forests to protected forest areas, whereas other less common indicator taxa were rare or absent in both.

It's important to clarify what may or may not be concluded from our results. First, our study is confined to southern Sweden, and our results should not be extrapolated to other parts of the country. Notably, however, a study based on data from SBS from boreal forests both with and without high natural values, had outcomes that were consistent with our results (Green, 2019). Green found that the four indicator species were similarly abundant, or more abundant, in forest areas located outside of forests with high natural values. Second, even though many individuals of the four species assessed showed territorial behavior in relatively young production stands, we do not know their absolute or relative breeding success in these habitats. Specifically, it remains unknown whether the habitat provided by intensively managed production stands are acting as population sources or sinks for these bird species (Pulliam, 1988). Evaluations of their nesting success in production forests relative to old growth natural forest stands is an important task for future studies. However, irrespective of whether production forest stands are acting as population sources or sinks, questions can nevertheless be raised regarding the suitability of continuing to use these species to indicate high conservation value forests.

Conclusions

Few studies have systematically surveyed bird populations in Sweden's production forest stands (but see our previous studies and Forslund, 2003), and the results from this study provide important new information regarding the most common terrestrial habitat category in Sweden, production forest stands. Because of the frequency with which these indicator taxa were encountered within these stands (almost 80% of production stands included at least one of the four indicator species), this raises important questions regarding the suitability of these species as indicators of forests of high conservation value. In order for the indicator species concept to function and be credible, the likelihood that the species occurs in habitats other than those to be indicated, has to be low (Lindenmayer & Likens, 2011) – something that is not the case with these four species. An important question can then be raised as to how the population trends of these four indicator species should be interpreted with respect to conservation efforts in production forests. If the four indicator species evaluated in this study have broader habitat requirements than previously inferred, then this challenges their suitability as indicators of older and high value forests. If, however, the production stands are acting as population sinks for these species, and successful breeding primarily takes place in old or high natural value forest, then positive trends in their abundance may in fact be indicative of positive trends in forest habitat availability. In either regard their regular exhibition of

territorial behaviour in structurally simplified, largely homogeneous production forest stands of <60 years, limits what can be concluded about the quality of forest habitat from their occurrence, and thus limits their potential use as indicators. Our results therefore raise important questions about how informative the population trends of these species may be in regards to ongoing development in the availability of these specific forest habitat types.

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References

- Ahti, T., Hamet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* **5**, 168.
- Allredge, M.W., Simons, T.R. & Pollock, K.H. (2007). A field evaluation of distance measurement error in auditory avian point count surveys. *J. Wildl. Mgmt.* **71**, 2759–2766.
- Andersson, C., Andersson, E. & Eriksson, A. (2018). *Indikatorer för miljö kvalitetsmålet levande skogar – dnr 2016/660*. Jönköping: Skogsstyrelsen.
- Andersson, C., Andersson, E., Blomqvist, S., Eriksson, A., Eriksson, H., Karlsson, S. & Roberge, J.-M. (2019). *Fördjupad utvärdering av levande skogar 2019*. Rapport 2019/2, Skogsstyrelsen.
- Benjamini, Y. & Hochberg, Y. (1995). Controlling the false discovery rate – a practical and powerful approach to multiple testing. *J. Roy. Stat. Soc. B* **57**, 289–300.
- Bibby, C.J., Burgess, N.D. & Hill, D.A. (2000). *Bird census techniques*. London: Academic Press.
- Brockhoff, E.G., Barbaro, L., Castagneryrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., Lyver, P.O.B., Meurisse, N., Oxbridge, A., Taki, H., Thompson, I.D., van der Plas, F. & Jactel, H. (2017). Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodivers. Conserv.* **26**, 3005–3035.
- Calladine, J., Jarrett, D., Wilson, M. & Edwards, C. (2017). Stand structure and breeding birds in managed Scots pine forests: some likely long-term implications for continuous cover forestry. *Forest Ecol. Manag.* **397**, 174–184.
- Cirule, D., Krama, T., Krams, R., Elferts, D., Kaasik, A., Rantala, M.J., Mierauskas, P., Luoto, S. & Krams, I.A. (2017). Habitat quality affects stress responses and survival in a bird wintering under extremely low ambient temperatures. *Sci. Nat.* **104**. <https://doi.org/10.1007/s00114-017-1519-8>.
- De Caceres, M. & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology* **90**, 3566–3574.
- Denny, R.E. & Summers, R.W. (1996). Nest site selection, management and breeding success of crested tits *Parus cristatus* at Abernethy forest, Strathspey. *Bird Study* **43**, 371.
- Diaz, S., Settle, J., Brondizio, E., Ngo, H., Guèze, M., Agard, J., Armeth, A., Balvanera, P., Ichii, K., Liu, J., Subramanian, S., Midgley, G., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R., Shin, Y., Visseren-Hamakers, I., Willis, K. & Zayas, C. (2019). *The global assessment report on biodiversity and ecosystem services*. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) – bit.ly/IPBESReport.
- Drever, M.C., Aitken, K.E.H., Norris, A.R. & Martin, K. (2008). Woodpeckers as reliable indicators of bird richness, forest health and harvest. *Biol. Conserv.* **141**, 624–634.
- Eggers, S. & Low, M. (2014). Differential demographic responses of sympatric parids to vegetation management in boreal forest. *Forest Ecol. Manag.* **319**, 169–175.
- Ekenstedt, J. & Olsson-Cipi, M. (2008). *Ekoparkplan rautiorova: Sveaskog*. Piteå: Sveaskog.
- Farmer, R.G., Leonard, M.L. & Horn, A.G. (2012). Observer effects and avian-call-count survey quality: rare-species biases and overconfidence. *Auk* **129**, 76.
- Forslund, M. (2003). *Fågelfaunan i olika skogsmiljöer – en studie på beståndsnivå*. Skogsstyrelsen rapport 2/2003.
- FSC. (2010). *Swedish FSC standard for forest certification including SLIMF indicators*. Uppsala: Forest Stewardship Council.
- Gosler, A. & Clement, P. (2019a). Coal tit (*Periparus ater*). In *Handbook of the birds of the world alive*. delHoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & deJuana, E. (Eds.). Barcelona: Lynx Edicions. Available at <https://www.Hbw.Com/node/59874>
- Gosler, A. & Clement, P. (2019b). Crested tit (*Lophophanes cristatus*). In *Handbook of the birds of the world alive*. delHoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & deJuana, E. (Eds.). Barcelona: Lynx Edicions. Available at <https://www.Hbw.Com/node/59878>
- Gosler, A., Clement, P. & Garcia, E.F.J. (2019). Willow tit (*Poecile montanus*). In *Handbook of the birds of the world alive*. delHoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & deJuana, E. (Eds.). Barcelona: Lynx Edicions. Available at <https://www.Hbw.Com/node/59860>
- Green, M. (2019). *Fåglar på standardrutten i och utanför skogliga värde trakter*. Lund: Svensk Fågeltaxering, Biologiska institutionen, Lunds Universitet.
- Green, M., Haas, F. & Lindström, Å. (2019). *Monitoring population changes of birds in Sweden*. Annual report for 2018: Department of Biology, Lund University. [In Swedish with English summary].

- Gustafsson, L. & Perhans, K. (2010). Biodiversity conservation in Swedish forests: Ways forward for a 30-year-old multi-scaled approach. *Ambio***39**, 546–554.
- Harrap, S. (2019). Eurasian treecreeper (*Certhia familiaris*). In *Handbook of the birds of the world alive*. delHoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & deJuana, E. (Eds.). Barcelona: Lynx Edicions. Available at <http://www.Hbw.Com/>
- Hofgaard, A. (1993). Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. *J. Veg. Sci.***4**, 601.
- delHoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & deJuana, E. (Eds.) (2017). *Handbook of the birds of the world alive*. Barcelona: Lynx Edicions. Available at <http://www.Hbw.Com/>
- Jansson, G. (1998). Guild indicator species on a landscape scale – an example with four avian habitat specialists. *Ornis Fennica***75**, 119.
- Johansson, T., Hjältén, J., deJong, J. & vonStedingk, H. (2013). Environmental considerations from legislation and certification in managed forest stands: a review of their importance for biodiversity. *Forest Ecol. Manag.***303**, 98–112.
- Jokimaki, J. & Solonen, T. (2011). Habitat associations of old forest bird species in managed boreal forests characterized by forest inventory data. *Ornis Fennica***88**, 57.
- Jonsson, B.G., Ekström, M., Esseén, P.-A., Grafström, A., Ståhl, G. & Westerlund, B. (2016). Dead wood availability in managed Swedish forests – policy outcomes and implications for biodiversity. *Forest Ecol. Manag.***376**, 174–182.
- Kouki, J. & Vaananen, A. (2000). Impoverishment of resident old-growth forest bird assemblages along an isolation gradient of protected areas in eastern Finland. *Ornis Fennica***77**, 145.
- Kuitunen, M. & Törmälä, T. (1983). The food of treecreeper *Certhia f. familiaris* nestlings in southern Finland. *Ornis Fennica***60**, 42.
- Kuuluvainen, T., Maki, J., Karjalainen, L. & Lehtonen, H. (2002). Tree age distributions in old-growth forest sites in Vienansalo wilderness, eastern Fennoscandia. *Silva Fenn.***36**, 169.
- Landres, P.B., Verner, J. & Thomas, J.W. (1988). Ecological uses of vertebrate indicator species – a critique. *Conserv. Biol.***2**, 316–328.
- Lewis, A.J.G., Amar, A., Cordi-Piec, D. & Thewlis, R.M. (2007). Factors influencing willow tit poecile montanus site occupancy: a comparison of abandoned and occupied woods. *The Ibis***149**, 205–213.
- Lindbladh, M., Hultberg, T., Widerberg, M.K. & Felton, A. (2011). Halland's forests during the last 300 years: a review of Malmström (1939). *Scand. J. Forest Res.***26**, 81–90.
- Lindbladh, M., Axelsson, A.-L., Hultberg, T., Brunet, J. & Felton, A. (2014a). From broadleaves to spruce – the borealization of southern Sweden. *Scand. J. Forest Res.***29**, 686–696.
- Lindbladh, M., Hedwall, P.-O., Wallin, I., Felton, A., Böhlenius, H. & Felton, A. (2014b). Short-rotation bioenergy stands as an alternative to spruce plantations: implications for bird biodiversity. *Silva Fenn.***48**. <https://doi.org/10.14214/sf.1135>.
- Lindbladh, M., Lindstrom, A., Hedwall, P.O. & Felton, A. (2017). Avian diversity in Norway spruce production forests – how variation in structure and composition reveals pathways for improving habitat quality. *For. Ecol. Manag.***397**, 48–56.
- Lindbladh, M., Petersson, L., Hedwall, P.O., Holmström, E. & Felton, A. (2019). Consequences for bird diversity from a decrease in a foundation species – replacing scots pine stands with Norway spruce in southern Sweden. *Reg. Environ. Change***19**, 1429–1440.
- Lindenmayer, B.D. & Franklin, J.F. (2002). *Conserving forest biodiversity: a comprehensive multiscaled approach*. Washington: Island Press.
- Lindenmayer, D.B. & Likens, G.E. (2011). Direct measurement versus surrogate indicator species for evaluating environmental change and biodiversity loss. *Ecosystems***14**, 47–59.
- Mikusinski, G., Gromadzki, M. & Chylarecki, P. (2001). Woodpeckers as indicators of forest bird diversity. *Conserv. Biol.***15**, 208–217.
- Müller, J. & Bütler, R. (2010). A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *Eur. J. Forest Res.***129**, 981–992.
- Nilsson, S.G. (1979). Effect of forest management on the breeding bird community in southern Sweden. *Biol. Conserv.***16**, 135–143.
- Nilsson, P., Roberge, C., Fridman, J. & Wulff, S. (2019). *Forest statistics 2019*. Umeå: Swedish University of Agricultural Sciences.
- Ottosson, U., Ottvall, R., Elmberg, J., Green, M., Gustafsson, R., Haas, F., Holmqvist, N., Lindström, Å., Nilsson, L., Svensson, M., Svensson, S. & Tjernberg, M. (2012). *Fåglarna i sverige – antal och förekomst*. Halmstad: SOF.
- Ottvall, R., Green, M. & Lindström, Å. (2006). *Häckande fåglar som rus-indikatorer för biologisk mångfald*. Jönköping: Länsstyrelsen i Jönköpings län.
- Patterson, I.J., Ollason, J.G. & Doyle, P. (1995). Bird populations in upland spruce plantations in northern Britain. *Forest Ecol. Manag.***79**, 107–131.
- Pulliam, H.R. (1988). Sources, sinks, and population regulation. *Am. Nat.***132**, 652–661.
- R Core Team. (2019). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Ram, D., Axelsson, A.-L., Green, M., Smith, H.G. & Lindström, Å. (2017). What drives current population trends in forest birds—forest quantity, quality or climate? A large-scale analysis from northern Europe. *Forest Ecol. Manag.***385**, 177–188.
- Roberge, J.M. & Angelstam, P. (2006). Indicator species among resident forest birds – a cross-regional evaluation in northern Europe. *Biol. Cons.***130**, 134–147.

- Rosenvald, R., Lohmus, A., Kraut, A. & Remm, L. (2011). Bird communities in hemiboreal old-growth forests: the roles of food supply, stand structure, and site type. *Forest Ecol. Manag.* **262**, 1541–1550.
- Rytter, L., Karlsson, A., Karlsson, M. & Stener, L.G. (2014). *Skötsel av björk, al och asp. Skogsskötselserien nr 9*. Jönköping: Skogsstyrelsen.
- SFIF. (2018). *Facts & figures*. Available at <https://www.forestindustries.se/forest-industry/facts-and-figures/>
- Skogsstyrelsen. (2019). *Statistik om formellt skyddad skogsmark, frivilliga avsättningar, hänsynsytor samt improduktiv skogsmark*. Hultgren, B. (Ed.). RAPPORT 2019/18 – DNR 2018/4167.
- Solonen, T. & Jokimäki, J. (2011). The efficiency of three-visit square surveys vs. one-visit line transects in censusing sparsely distributed birds in managed forest landscapes. *Bird Conserv. Int.* **21**, 156.
- Summers, R.W. (2007). Stand selection by birds in scots pinewoods in Scotland: the need for more old-growth pinewood. *The Ibis* **149**, 175–182.
- Summers, R.W., Mavor, R.A., Buckland, S.T. & MacLennan, A.M. (1999). Winter population size and habitat selection of crested tits *Parus cristatus* in Scotland. *Bird Study* **46**, 230.
- Suorsa, P., Huhta, E., Jantti, A., Nikula, A., Helle, H., Kuitunen, M., Koivunen, V. & Hakkarainen, H. (2005). Thresholds in selection of breeding habitat by the Eurasian treecreeper (*Certhia familiaris*). *Biol. Cons.* **121**, 443–452.
- Toms, J.D., Schmiegelow, F.K.A., Hannon, S.J. & Villard, M.A. (2006). Are point counts of boreal songbirds reliable proxies for more intensive abundance estimators? *Auk* **123**, 438.
- Vatka, E., Kangas, K., Orell, M., Lampila, S., Nikula, A. & Nivala, V. (2014). Nest site selection of a primary hole-nesting passerine reveals means to developing sustainable forestry. *J. Avian Biol.* **45**, 187–196.
- Versluijs, M., Hjältén, J. & Roberge, J.M. (2019). Ecological restoration modifies the value of biodiversity indicators in resident boreal forest birds. *Ecol. Indic.* **98**, 104–111.
- Virkkala, R., Rajasarkka, A., Vaisanen, R.A., Vickholm, M. & Virolainen, E. (1994). Conservation value of nature-reserves – do hole-nesting birds prefer protected forests in southern Finland. *Ann. Zool. Fenn.* **31**, 173.
- Williams, L. & Ellis, C.J. (2018). Ecological constraints to 'old-growth' lichen indicators: Niche specialism or dispersal limitation? *Fungal Ecol.* **34**, 20–27.