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Avian diversity in Norway spruce production forests – How variation in structure and composition reveals pathways for improving habitat quality

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ABSTRACT

Forests used for timber production provide essential ecosystem services to society, as well as potential breeding habitat for bird communities. In southern Sweden, 90% of productive forest land is used for timber production and stands dominated by Norway spruce (*Picea abies*) constitute approximately 40% of the forested area. Due to their homogeneous structure, these spruce production forests are often regarded as depauperate. Despite this perception, knowledge about the biodiversity found in these stands is scarce. Here we synthesize the results of four separate bird surveys conducted within 35 spruce production stands of southern Sweden. The results are compared to recent population trends within the general study area. In total 49 bird species were recorded, with a strong difference in species composition between newly planted clear-cuts (forest age <15 years) and forests older than 15 years. The majority of species encountered in the older forest category were common forest birds, with a single red-listed species among the regularly occurring species. In contrast, three red-listed "farmland species" were frequently encountered in the newly planted forests, revealing the capacity of those birds preferring open and recently disturbed habitats to utilize clear-cuts. A higher diversity of tree sizes and the inclusion of even relatively small proportions (<15%) of broadleaved tree species had a positive effect on bird species richness. Several species encountered in spruce production forests are declining in numbers, but it is not clear whether these stands are acting as source or sink environments for their populations. However, our results indicate that relatively small adjustments to spruce forest management should improve the quality of this widespread habitat.

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1. Introduction

Forests used for timber production are increasing in extent and now constitute one third of global forest area (FAO, 2010). Besides providing important ecosystem services to society, these forests also provide habitat for plants and animals (Pawson et al., 2013). In Sweden, 90% of productive forest land is used for timber production (Anonymous, 2016), and the primary approach to forest management involves the rotational clear-cutting of even-aged coniferous stands. Over the last 100 years the increased use of this forest management model, as well as changes in agricultural practices, have dramatically altered tree species composition especially in the southern parts of the country (Lindbladh et al., 2014a).

Norway spruce (*Picea abies*, hereafter spruce), has benefited most from this alteration in Sweden, to the extent that spruce dominated stands cover approximately 40% of the forested area (Anonymous, 2016). Forest managers have promoted spruce due to its simple management, early returns from thinning, high wood production, short rotation periods, low susceptibility to browsing pressure from ungulates (Månsson et al., 2007) and favorable market demand. A development of a "spruce culture" among forest managers (Felton et al., 2010a) has further strengthened the promotion of spruce.

Due to their homogeneous structure, intensively managed spruce production forests are often regarded as depauperate habitats (Gärdenfors, 2015). Whereas this perception may be warranted, especially in relation to natural forest systems, there is nevertheless a lack of studies of species diversity, including bird communities, in these stands (but see Nilsson, 1979a, b; Felton et al., 2011). This is unfortunate because societies require evidence-based evaluations of the biodiversity contribution of

dominant land-uses. Birds are a particularly advantageous taxonomic group for biodiversity assessments (e.g. Fischer et al., 2007) because they fulfill diverse and important ecological functions, including seed dispersal, pest control, pollination, and ecosystem engineering (Sekercioglu, 2006). Furthermore, birds are also visually and acoustically conspicuous (Whelan et al., 2008), and can thus provide an efficient means of evaluating the importance of habitat structure and change in forest systems (Gardner et al., 2008).

To increase the knowledge regarding the avian diversity found in spruce production forests, we synthesize data from four surveys conducted in 35 spruce production stands of varying age in southern Sweden. As the composition and abundance of bird communities can be affected by the management of the stands (e.g. rotation length, (Jansson and Andrén, 2003), the proportion of conifer versus broadleaved trees (Felton et al., 2010b) and the stand's structural diversity (MacArthur, 1964)), we were particularly interested in the influence of such factors on bird numbers and species diversity. The specific questions addressed in this study are:

- Which bird species dominate this forest habitat during the breeding season?
- How does species number and composition relate to stand age?
- How are bird species composition and abundance affected by different levels of broadleaves in the spruce stands?
- Do stands with a more diverse diameter distribution have a higher diversity and distinct bird species composition?

We then compare our data to the breeding population trends for the same species and region, as recorded in standardized counts of the Swedish Bird Survey (SBS, Green et al., 2016). These trends provide an important context for evaluating the contribution that spruce production stands make to habitat availability in the region. The SBS is designed to capture general trends in bird species occurrence and abundance, but in contrast to this study, do not relate survey outcomes to specific habitats or vegetation types.

In summary, the overall goal of the study is to provide information to forest owners and policy makers about the value of Norway spruce production forests for breeding bird communities, and how management interventions can detract or enhance this value. Our results are of relevance outside of Sweden, as Norway spruce is commonly used in the production forests of other northern and central European countries

2. Methods

We used data from four studies, surveyed during 2010, 2011, 2013 and 2016 respectively, two of which were published (Felton et al., 2011; Lindbladh et al., 2014b). Each study had a different purpose; two investigated the influence of a deciduous component in spruce forests, and one surveyed young stands. The fourth survey (from 2016) was conducted in order to provide a more balanced and representative data set for analysis, with respect to stand age and the relative proportion of deciduous trees.

2.1. Study area

The 35 surveyed stands (Fig. 1) are located in the hemi-boreal and temperate zones of southern Sweden (Ahti et al., 1968).

The mean temperature (1961–1990) in the region ranged between −2 and −3 °C in January, and between 14 °C and 15 °C in July. Precipitation varies widely between the western part (1000–1200 mm/year) and the eastern part (approximately 600 mm/year) of the study area.

Forests cover 63% of the land area in southern Sweden (Götaland). Commercial forestry dominates, and approximately 2% of productive forest land is formally protected (Table 1.5 in Nilsson and Cory, 2016). Norway spruce is the most common tree species, comprising 47% of total volume (SFA, 2014). Norway spruce dominated forests are generally managed using rotationally clear cut even-aged stands which are pre-commercially and commercially thinned two to three times during a rotation, and are harvested after a rotation period of between 45 and 70 years. Scots pine (*Pinus sylvestris*) is the second most common tree (33%) in the region, followed by birch (*Betula pendula/pubescens*; 11%) oak (*Quercus robur/petraea*; 3.3%), aspen (*Populus tremula*; 2.6%), alder (*Alnus glutinosa*; 2.4%) and beech (*Fagus sylvatica*; 1.6%).

2.2. Bird surveys

Stands ranged in size from 4.0 to 23.5 ha, with a mean stand size of 10.0 ha ±5 SD. All four studies used the point count method to survey the breeding bird communities in these stands (Bibby et al., 2000). Point counts are an effective means of surveying bird communities, with the abundance estimates provided acting as indices that are correlated with the true abundance of the bird species present (Felton et al., 2016b). Each study used the same methodology, with the exception that the size of the point count area surveyed varied between studies. In two of the studies the survey radius was 40 m, whereas it was 50 m in the other two. These threshold distances limit the birds assessed to only those located within the stand, and reduce the risk of double counting birds at two survey points. Furthermore, this radius is less than the maximum distance observers are estimated to be able to differentiate the distance to calling birds (i.e. 65 m, see Alldredge et al., 2007). Four survey points were located within each stand (each of the four points were surveyed four times, see below), with the proviso that the distance between two survey points was 80 or 100 m (depending on study, see above), and at least 40 m from the stand edge. Points were concentrated within the centre of each stand, to reduce the influence of birds using the transition zone of vegetation at the edge of the study site. This constraint also helped to ensure that survey points were not displaced over larger areas in larger stands, which could have increased bird community diversity in such stands due to an increased range of environments surveyed. Survey points were located beforehand using aerial photos and the aforementioned decision rules, to avoid onsite selection bias. Whereas modeling approaches can be used to address detectability issues in point count data, these approaches themselves introduce additional concerns and uncertainties (Barry and Welsh, 2001; Johnson, 2008). In this study we adopt an *a priori* approach to minimizing problems of detectability in the field via multiple elements of our sampling design (see below).

We surveyed each of the study sites four times; twice in early spring (April) and twice in late spring (May/June). We chose these survey periods to coincide with annual peaks in singing activity of breeding resident and migrant passerines respectively. Notably, the majority of the tropical migrant passerines surveyed have not arrived in this region at the time of the first survey period. Daily surveys began at dawn, at approximately 6:00 am in April and 4:30 am in May/June, and finished at 9:00 am and 7:30 am respectively. This period overlapped with the daily peak in bird vocal activity. On each survey day, the same person surveyed two stands. The order in which the stand types were visited each day was varied systematically to ensure that no stands types were weighted towards early morning or late morning survey times. Surveys were only conducted in suitable weather for conducting bird surveys (i.e. minimal wind, no rain), to minimize environmental influences on detectability.
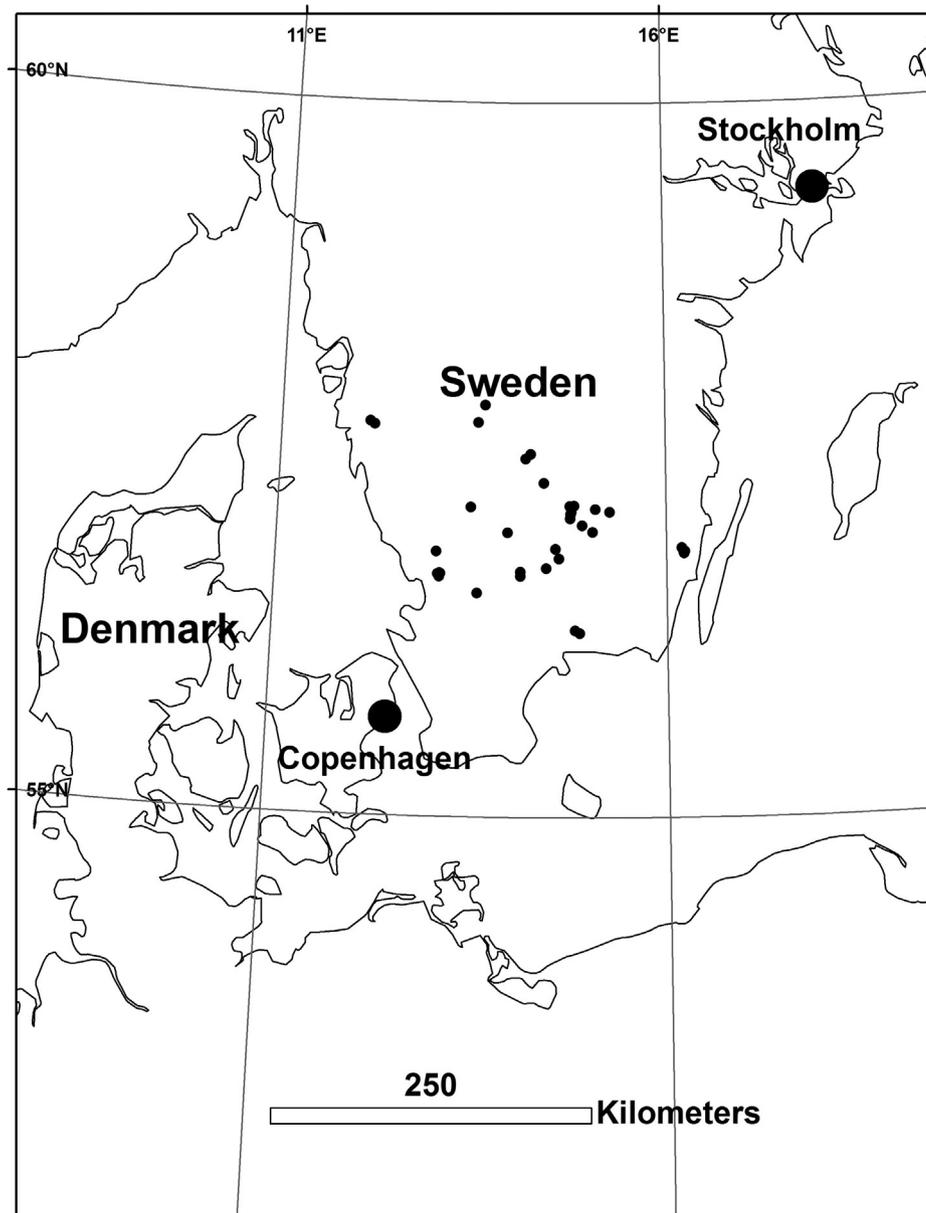
Fig. 1. Map of southern Sweden with all surveyed sites shown.

All point count surveys were conducted by ornithologists (AF, ML, Erik Andersson, and Thomas Nyberg) experienced with both bird identification and point count surveys, a combination of skill sets which are important for repeatability (Farmer et al., 2012). The stands were randomized among the observers, and each point was surveyed for five minutes (Bibby et al., 2000). Most identification was made acoustically rather than visually. In cases of uncertainty (e.g. an individual bird shifting among survey points during the survey), the most conservative estimate of abundance was used. Birds observed flying overhead were not included in the survey.

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. We adopted this approach as research indicates that true avian abundance is best correlated with maximum rather than average abundance data from repeated surveys (Toms et al., 2006). This approach also accounts for seasonal differences in the song activity (and therefore detectability) of resident

and migrant bird species. As the area surveyed differed between the studies (40 vs. 50 m radius), all bird data was converted to individuals per hectare.

We also evaluated the conservation status and ecological characterics of the bird species encountered. To do so we assessed the current threatened status of each species encountered using the Swedish Red List (Gärdenfors, 2015). Bird species migratory status, food guilds, nest site and forest preferences were derived from the Birds of the Western Palearctic (BWPi, 2007) and are presented in Appendix A.

2.3. Vegetation surveys

We conducted surveys of vegetation structure during the same year as the bird surveys. The size of all trees ≥ 2 cm were measured and tree species noted in an area of 1256 m^2 (circle) in the stands >15 years of age, and in an area of 530 m^2 in the young stands ($\leq$15 years old). The young stands in our study were heavily dominated by broadleaves (mostly birches), but this is indicative of

conditions associated with the early rotation stages of spruce monoculture forest management in this region (Holmström et al., 2016). The majority of these naturally regenerated broadleaved tree species, as well as other competing vegetation, is actively removed during a pre-commercial thinning, which takes place less than ten years after establishment.

The age of the 35 stands varied from approximately 7 years to a maximum of 90 years of age, with an average age of 34 years (Appendix B). Stand basal area varied between 0.2 and 21.5 m^2 in young stands and between 22.6 and 54.2 m^2 in stands >15 years of age. The proportion of the basal area consisting of Norway spruce varied between 11 and 94% in the young stands, and between 76 and 100% in stands >15 years old. The broadleaved component was between 1 and 91% in the young stands and between 0 and 24% in the >15 years old stands, with the vast majority of broadleaved trees consisting of birch. No trees had a DBH >20 cm in the young stands, and one young stand had no trees ≥2 cm. The largest trees in the stands >15 years old had a DBH of >70 cm. The average number of stems was 1245 stems ha^{-1} in the young stands and 904 stems ha^{-1} in the stands >15 years old.

2.4. Swedish Bird Survey

We relate our results to trends in bird species regional abundance since 1998, as provided by the Swedish Bird Survey (SBS). To do so we used data from the fixed routes of the Swedish Bird Survey (Green et al., 2016; Ram et al., 2017). The scheme consists of 716 routes, each 8 km long, distributed evenly over Sweden in a grid of 25 km. In this way, birds are surveyed within a representative sample of Sweden's different natural habitats, including a wide variety of different forest types. For the analyses we used the total number of individuals of a given bird species seen per route and year. To ensure overlap with the study region of our spruce forest surveys, we used the observations from the 86 most proximate routes in the counties of Blekinge, Halland, Kalmar, Kronoberg, Jönköping, and the southern part of Västra Götaland.

2.5. Statistical analyses

All statistical analyses on the bird surveys in spruce forests were done in R 3.2.2 (R Core Team 2015). To analyse the effects of stand age on bird communities an unconstrained ordination, non-metric multidimensional scaling (NMS), was performed on the bird community data by applying the metaMDS function in the Vegan package (Oksanen et al., 2016). The correlation between site locations in ordination space and the abundance-weighted share of birds within life history trait categories, together with abundance weighted share of increasing, decreasing or stabile populations from the SBS, were analysed by the envfit function and projected on the final NMS solution. The output illustrates the strength (length of arrows) and the direction of the strongest correlation. The NMS and projection of environmental variables were done with Bray–Curtis dissimilarity and 999 permutations. An NMS was likewise used to describe the effects of stand age on the functional bird composition. In this NMS the relative distribution between traits within the sites was used as the "species data".

The effects of stand characteristics on species richness and species evenness (how close in numbers the different species in an environment are) was modelled using Generalized Linear Models (GLM) with a Poisson or Gamma error distribution, respectively, both with log-links. When all data was included many stand parameters were correlated with stand age. Older stands had higher basal area (r^2 = 0.71), lower share of broadleaved tree species (r^2 = 0.59) and higher structural diversity (r^2 = 0.71), than younger stands. To avoid problems with multicollinearity all data were included only in a model of the effect of stand age. For further

analysis, young stands (≤15 years old) were excluded, which removed all collinearity problems. Likewise there were no differences between surveys concerning the variables used to describe stand structure (P = 0.139–0.682 from ANOVAs). The linear effects of basal area, share of broadleaved tree species, number of tree species and structural diversity (Shannon diversity of the tree size classes) on bird species richness, were modelled using separate GLMs to avoid problems with over-parameterization. The full GLMs included a year effect as a factorial variable with four levels and a correction for spatial autocorrelation. The latter was introduced into the models as a two-dimensional smoother of the spatial coordinates of the stands. Akaike Information Criterions (AIC) was compared for five different models: (1) stand variable + year effect + spatial correlation, (2) stand variable + year effect, (3) stand variable + spatial correlation, (4) stand variable, (5) year effect, and the model with the lowest AIC was chosen as the most appropriate. In the GLMs including all data the effects of the squared stand age was included to account for non-linear patterns. Here no year effect could be included due to the collinearity patterns in the data. The GLMs were conducted using the gam function in the mgcv package to facilitate the use of smoothers for the spatial coordinates (Wood and Wood, 2016).

The SBS trends were calculated using TRIM (Trends & Indices for Monitoring data, v.3.53, Pannekoek and van Strien, 2004), which is the standard analysis tool used in the Pan-European Common Bird Monitoring Scheme. A Poisson log-linear regression is used to estimate species-specific yearly indices and temporal trends in annual abundance, controlling for serial correlation and over-dispersion, using the model "Time effects" (model 3, or "Effects for each time point") in the program. The basic TRIM model is: expected count = year + site, where both year and site are fixed effects.

3. Results

3.1. Bird survey result

In total 49 bird species were recorded during the surveys, 30 in the young stands (≤15 years old) and 38 in the stands > 15 years old (Appendix C). In the 14 young stands, Willow warbler (*Phylloscopus trochilus*), Great tit (*Parus major*), Yellowhammer (*Emberiza citrinella*), Meadow pipit (*Anthus pratensis*) and Garden warbler (*Sylvia borin*), in that order, had the highest average number of individuals per ha (Table 1). In the >15 years old stands, Chaffinch (*Fringilla coelebs*), Goldcrest (*Regulus regulus*), Eurasian siskin (*Spinus spinus*), Robin (*Erithacus rubecula*) and Treecreeper (*Certhia familiaris*) were the most commonly encountered species (Table 1).

The NMS unconstrained ordination resulted in a solution requiring only two-dimensions. The ordination diagram shows clear differences in ordination space for young stands (≤15 years old) and the stands >15 years old, and thus indicated differences in the species composition of their respective bird communities (Fig. 2a).

The share of migrants, ground nesters and insectivores were positively correlated with the first dimension, whereas partial migrants, off ground nesters and granivores were negatively correlated with that dimension (Table 2).

The shares of residents and cavity nesters showed a low correlation with the first dimension but were positively correlated with the second. For omnivores there was no significant correlation. The young stands had, with some exceptions, high scores on the first axis, and hence insectivores, migrants and ground nesters were associated with these stands. The older stands were aggregated to the lower-left in the ordination space, and granivores, off-ground nesters, partial migrants, residents, and cavity nesters, as well as species decreasing in the SBS, were associated with these

Table 1

The number of individuals per ha from surveys in the two forest age types (Standard deviation within brackets), and each species' threat level according to the Swedish Red-list. NT is Near Threatened, VU is Vulnerable. The regional trend for each species according to the SBS (%, annual change rate), and the significance level of the trend (Sign) in the period 1998–2015 are also shown. An asterisk after the name denote species almost exclusively associated with coniferous forests.

	Young stands (≤15 yr old)					Stands >15 yr old			
	Ind ha^{-1}	Threat level	%	Sign		Ind ha^{-1}	Threat level	%	Sign
Willow warbler (*Phylloscopus trochilus*)	1.28 (0.97)		0.2	NS	Chaffinch (*Fringilla coelebs*)	2.29 (1.06)		−1.3	***
Great tit (*Parus major*)	0.43 (0.41)		3.5	***	Goldcrest* (*Regulus regulus*)	1.45 (0.69)	VU	−3.6	***
Yellowhammer (*Emberiza citrinella*)	0.39 (0.38)	VU	−1.4	***	Eurasian siskin* (*Spinus spinus*)	1.09 (1.46)		−2	***
Meadow pipit (*Anthus pratensis*)	0.36 (0.61)	NT	2	NS	Robin (*Erithacus rubecula*)	0.97 (1.02)		−0.3	NS
Garden warbler (*Sylvia borin*)	0.25 (0.36)		0.4	NS	Treecreeper (*Certhia familiaris*)	0.56 (0.55)		1.4	NS
Tree pipit (*Anthus trivialis*)	0.25 (0.31)		1.2	**	Coal tit* (*Periparus ater*)	0.50 (0.41)		0.2	NS
Whinchat (*Saxicola rubetra*)	0.21 (0.31)	NT	0.8	NS	Great tit (*Parus major*)	0.48 (0.47)		3.5	***
Robin (*Erithacus rubecula*)	0.18 (0.36)		−0.3	NS	Song thrush (*Turdus philomelos*)	0.47 (0.37)		1.7	***
Eurasian jay (*Garrulus glandarius*)	0.14 (0.40)		0.4	NS	Wren (*Troglodytes troglodytes*)	0.38 (0.43)		2	***
Red-backed shrike (*Lanius collurio*)	0.11 (0.28)		0.9	NS	Willow warbler (*Phylloscopus trochilus*)	0.30 (0.72)		0.2	NS
Lesser whitethroat (*Sylvia curruca*)	0.11 (0.20)		−0.4	NS	Blackbird (*Turdus merula*)	0.28 (0.36)		0.1	NS
Blackbird (*Turdus merula*)	0.11 (0.20)		0.1	NS	Willow tit* (*Poecile montanus*)	0.21 (0.25)		2.5	*
Chaffinch (*Fringilla coelebs*)	0.11 (0.20)		−1.3	***	Woodpigeon (*Columba palumbus*)	0.21 (0.31)		3.2	***
Mistle thrush* (*Turdus viscivorus*)	0.07 (0.26)		3	***	Dunnock* (*Prunella modularis*)	0.20 (0.35)		−0.7	NS
Wryneck (*Jynx torquilla*)	0.07 (0.17)		6.7	***	Bullfinch* (*Pyrrhula pyrrhula*)	0.14 (0.28)		5	***
Great spotted woodpecker (*Dendrocopos major*)	0.07 (0.17)		3.3	***	Eurasian jay (*Garrulus glandarius*)	0.14 (0.28)		0.4	NS
Goldcrest* (*Regulus regulus*)	0.07 (0.26)		−3.6	***	Tree pipit (*Anthus trivialis*)	0.08 (0.15)		1.2	**
Eurasian siskin (*Spinus spinus*)	0.07 (0.26)		−2	***	Blue tit (*Cyanistes caeruleus*)	0.08 (0.22)		3.2	***
Blackcap (*Sylvia atricapilla*)	0.04 (0.13)		6.2	***	Wood warbler (*Phylloscopus sibilatrix*)	0.08 (0.17)		0.5	NS
Blue tit (*Cyanistes caeruleus*)	0.04 (0.13)		3.2	***	Blackcap (*Sylvia atricapilla*)	0.06 (0.16)		6.2	***
Common whitethroat (*Sylvia communis*)	0.04 (0.13)		1.2	**	Crossbill* (*Loxia* ssp.)	0.06 (0.13)		2.7	NS
Crested tit* (*Lophophanes cristatus*)	0.04 (0.13)		0.6	NS	Crested tit* (*Lophophanes cristatus*)	0.05 (0.11)		0.6	NS
Green woodpecker (*Picus viridis*)	0.04 (0.13)		0.8	NS	Greenfinch (*Chloris chloris*)	0.03 (0.09)		−1.6	**
Linnet (*Linaria cannabina*)	0.04 (0.13)		−1.7	*	Mistle thrush* (*Turdus viscivorus*)	0.03 (0.09)		3	***
Reed bunting (*Emberiza schoeniclus*)	0.04 (0.13)		−1	NS	Nuthatch (*Sitta europaea*)	0.03 (0.14)		2.9	***
Song thrush (*Turdus philomelos*)	0.04 (0.13)		1.7	***	Redwing (*Turdus iliacus*)	0.03 (0.09)		−5.6	***
Willow tit* (*Poecile montanus*)	0.04 (0.13)		2.5	*	Black woodpecker (*Dryocopus martius*)	0.02 (0.11)		−0.7	NS
Woodcock (*Scolopax rusticola*)	0.04 (0.13)		2	NS	Great spotted woodpecker (*Dendrocopos major*)	0.02 (0.11)		3.3	***
Woodpigeon (*Columba palumbus*)	0.04 (0.13)		3.2	***	Nutcracker* (*Nucifraga caryocatactes*)	0.02 (0.11)	NT	No trend	
Nutcracker* (*Nucifraga caryocatactes*)	0.04 (0.13)		No trend		Pied flycatcher (*Ficedula hypoleuca*)	0.02 (0.11)		1.7	***
					Woodcock (*Scolopax rusticola*)	0.02 (0.11)		2	NS
					Chiffchaff (*Phylloscopus collybita*)	0.02 (0.07)		15.8	***
					Long-tailed tit (*Aegithalos caudatus*)	0.02 (0.07)		2.1	NS
					Raven (*Corvus corax*)	0.02 (0.07)		−0.6	NS
					Sparrowhawk (*Accipiter nisus*)	0.02 (0.07)		4.4	***
					Treesparrow (*Passer montanus*)	0.02 (0.07)		6.7	*
					Yellowhammer (*Emberiza citrinella*)	0.02 (0.07)	VU	−1.4	***

stands. The ordination of the traits shows that the young stands, in addition to differing in taxonomical composition, also differed with respect to functional traits (Fig. 2b), with only a small overlap with the mid-aged stands (15–49 years).

The model with the lowest AIC of the effect of stand age on species richness included a non-linear effect of stand age (P = 0.009), and a correction for spatial correlation (P = 0.025). Stand age had a significant positive effect on species richness up to around 60 years (Fig. 3). The decline after that is statistically uncertain due to large standard errors. The model with the lowest AIC of the effect of stand age on species evenness included a linear effect of stand age (P = 0.003) and a correction for spatial correlation (although the latter was not significant, P = 0.178). The species evenness decreased linearly (on the log-scale) with increasing stand age (Fig. 3) most likely because older stands had more species that occurred at low abundance.

As the youngest stands (≤15 years old) differed in many aspects compared to the older stands, in particular with respect to the relative abundance of broadleaved trees, we excluded them in the following analyses. There was a positive effect of the share of broadleaves and the diversity of tree sizes classes on species richness, despite a significant year effect (Table 3, Fig. 3). The diversity

of tree size classes and the amount of broadleaves were uncorrelated, indicating that these factors affect the species richness independently. Bird species richness was not affected by basal area or the number of tree species with more than 1% of basal (Table 3).

3.2. Swedish Bird Survey & the red-list

The bird species found in our study show varying trends in the Swedish Bird Survey within the study area (Green et al., 2016) (Table 1). Regarding the stands >15 years old, the three most common species in this study (Chaffinch, Goldcrest and Siskin), have decreasing trends in the SBS (Table 1), and one of them, Goldcrest, was recently red-listed (Near Threatened, (Gärdenfors, 2015). Only three of the remaining species found in the old stands show significant decreasing trends, with the majority of the bird species encountered increasing in abundance in the region since 1998. Regarding the nine species largely confined to coniferous forests, only Goldcrest and Siskin have significant negative trends, with the remaining exhibiting stable or increasing population trends over recent decades (Table 1).

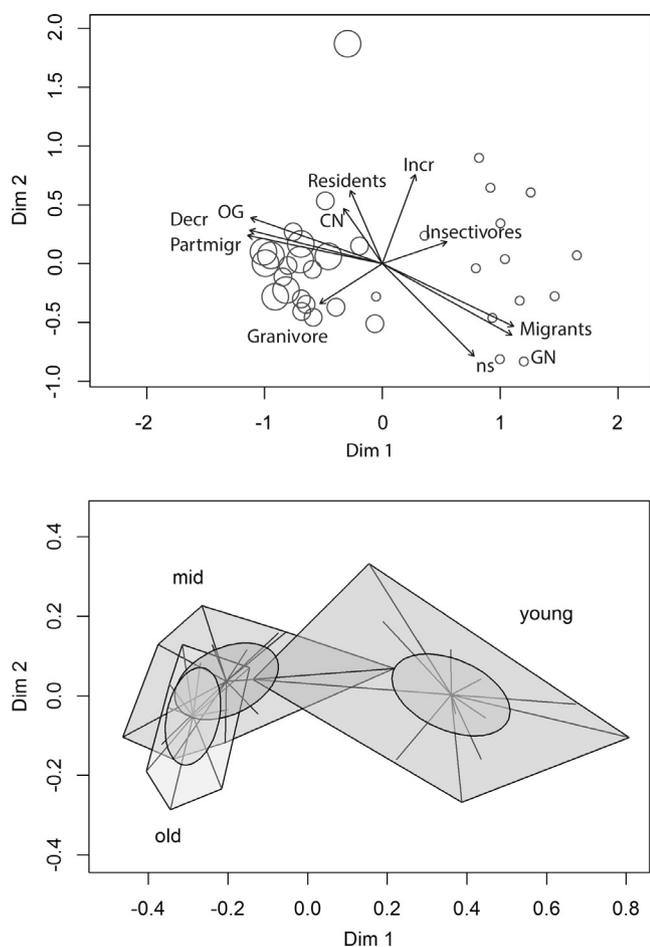The three most common bird species in the young stands (≤15 years old) show varying trends in SBS (Table 1). Willow

	NMDS1	NMDS2	r2	Pr (> r)
Residents	−0.40	0.92	0.26	0.008[**]
Migrants	0.90	−0.43	0.85	0.001[***]
Part. migrants	−0.98	0.21	0.85	0.001[***]
Insectivores	0.95	0.32	0.19	0.037[*]
Omnivores	0.91	0.42	0.01	0.873
Granivores	−0.84	−0.54	0.22	0.020[*]
Cavity nesters	−0.57	0.82	0.18	0.029[*]
Ground nesters	0.88	−0.48	0.88	0.001[***]
Off-ground nesters	−0.94	0.33	0.78	0.001[***]
Decreasing species	−0.97	0.24	0.75	0.001[***]
Stable (ns) species	0.7	−0.71	0.68	0.001[***]
Increasing species	0.35	0.94	0.36	0.001[***]

Fig. 2. (a) NMS ordination of all plots and species. Abundance weighted shares of birds within trait categories and population trends with significant correlations (p < 0.05) with the NMS are projected on the ordination. The age of the sites are indicated by the size of the circles (Young < 15, Mid 15–49 and Old 50+ years old), i.e. the size is increasing with age. GN is ground nesters, CN cavity nesters and OG off ground nesters, Decr is decreasing species, Incr is increasing species, and ns is stable or without significant population change in the SBS. (b) The NMS ordination of the functional traits. The stands are divided in three groups according to their age (young < 15, mid 15–49 and old 50+ years old). The groups total distribution in the "functional space" is marked together with the centroids and the ellipse show the 95% confident intervals.

warbler shows no trend, Great tit a positive trend, and Yellowhammer a negative trend. Yellowhammer (VU), Meadow pipit (NT), and Whinchat (*Saxicola rubetra*) (NT) were encountered in relatively large numbers in the young stands, and are red-listed (Gärdenfors, 2015). Note however that in those studies in which the breeding behaviour of species were noted, Meadow pipits were only recorded as calling (and not singing), and thus may have only been using these stands during migration. Of these three species only Yellowhammer show a significant negative trend in the SBS. Two other bird species encountered in fewer numbers in the young stands show a significant negative trend in SBS, they are Chaffinch and Linnet. Few of the birds found in the young stands are conifer associated, with those encountered only occurring in limited numbers.

4. Discussion

Considering that the surveyed production stands provide a very common forest cover in Sweden, it is not surprising that the most frequently encountered species in the young stands (Willow warbler) and the >15 year old stands (Chaffinch), are the most abundant species in Sweden (Ottosson et al., 2012). Only a few individuals of species of conservation concern were encountered in the >15 year old stands, including the Goldcrest which was recently red-listed due to sustained population declines (Ottosson et al., 2012; Green et al., 2016). A larger number of red-listed and relatively uncommon species were found in the young stands. As could be expected, we found that young plantations (≤15 years old) harboured a distinct bird species composition compared to the older stands. Many of the birds in the young stands are ground nesters, insectivores and migrants, which most probably benefited from the many broadleaves and the open, sunny conditions. The predominance of migrants in these stands presumably results from the greater capacity of many migrant bird species to utilize disturbed forests and early succession forest cover (Helle and Fuller, 1988; Hansson, 2001). Later in the rotation cycle, and as indicated in the >15 years old stands, environmental conditions developed to tip the balance in favor of resident bird species. Interestingly however, even if the young stands represent a simplified habitat compared to natural young forests after a disturbance, among the most frequently encountered species in the young stands were several open-land associated red-listed taxa. These were Yellowhammer, Meadow pipit (note caveat above) and Whinchat. These three species are considered "farmland birds" in Sweden, although substantial numbers of their populations occur outside of farmlands, such as forest clear-cuts, bogs and mires (Stjernman et al., 2013). Consistent with this finding, a recent study in Poland found forest clear-cuts to harbour a substantial number of farmland birds, inclusive some that declining species such as the Yellowhammer (Zmihorski et al., 2016). Yellowhammer has been decreasing in our study region according to the SBS, whereas Whinchat and Meadow pipit exhibit no significant trend in their population numbers (Table 1). The reason why several "farmland species" are experiencing population declines in Sweden is the combined effect of intensification of agricultural land-use and the abandonment of unproductive farmland (Wretenberg et al., 2006). The wide availability of young spruce plantations raises the possibility that the presence of clear-cuts is compensating for the loss of farmland-associated habitat elsewhere, and could thereby help mitigate general population declines of those "farmland birds" capable of exploiting these environments (Söderström and Karlsson, 2011; Żmihorski et al., 2016). Alternatively, young spruce stands may in fact represent substandard habitat for farmland birds, thereby acting as potential population sinks rather than sources for these species. Unfortunately there are no published studies on the reproductive success of these particular farmland species in this habitat. However, two studies have been conducted on the Red-backed shrike, which is a farmland-associated species which can on occasion be found
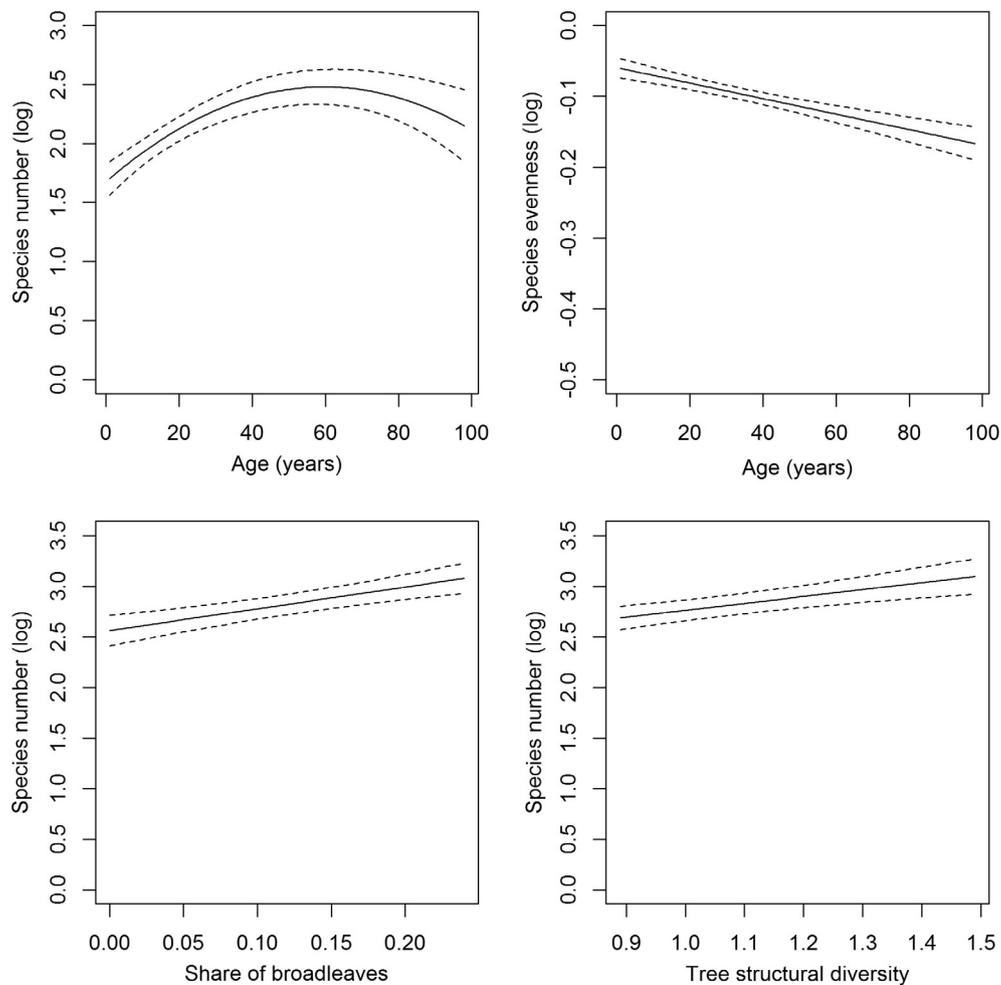
Fig. 3. Top left: Predicted values of species number and relative to stand age (and 95% CI) from the Generalized Linear Models, all stands included. Top right: Predicted values of species evenness relative to stand age and 95% CI from the Generalized Linear Models, all stands included. Lower left: Species richness as a function of share of broadleaves, in >15 years stands only. Lower right: Species richness as a function of Shannon diversity of tree sizes classes, >15 year old stands only.

Table 3
P-values from the Generalized Linear Models of the effect of stand structure on species richness chosen by AIC. Only stands >15 years old are included. Tree Shannon is Shannon diversity of tree sizes classes.

	p-value	p-value (year effect)
Share of broadleaves	0.020	0.003
Tree Shannon	0.043	<0.001
Basal area	–	<0.001
Number of tree species (with >1% of basal area)	–	<0.001

breeding on clearcuts. Söderström and Karlsson (2011) surveyed the reproductive performance of this species and found that the average survival of fledglings and post-fledging was significantly higher in clear-cuts than in grasslands, presumably due to lower nest predation in the clear-cuts. However, Hollander et al. (2013) found the opposite result in their assessment of reproductive performance of this species in clearcuts vs. traditional farmland habitat. Evidently, to elucidate if young production forests are sources or sinks, more studies are needed on both the Red-backed shrike and other farmland birds using clearcuts as breeding habitat.

In the stands >15 years old, the three most common species were Chaffinch, Goldcrest, and Siskin. All three of these species exhibit negative population trends in the region according to SBS, with the Goldcrest recently being red-listed (Gärdenfors, 2015).

The relative high abundance of these species in spruce production forests shows that this is a regularly utilized habitat for this species. However, as noted above with respect to the occurrence of farmland birds in young stands, it also remains unclear whether the >15 years old stands actually constitutes a source or sink habitat for these declining species.

According to our analysis bird species richness increased, and evenness decreased, with stand age. Richness and evenness are to some extent connected as higher numbers of species increases the possibility for the occurrence of rare species, and hence for decreasing evenness. Our finding that species richness increased with stand age is not surprising, and has been shown in many studies (Edenius and Elmberg, 1996; Nikolov, 2009). In many of the >15 years old stands we encountered several species considered to be "forest specialists", i.e. species with higher demands on forest quality (Ram et al., 2017). These species included Coal tit (*Periparus ater*), Willow tit (*Poecile montanus*), Treecreeper (*Certhia familiaris*), Crested tit (*Lophophanes cristatus*) and Bullfinch (*Pyrrhula pyrrhula*), though the latter two were encountered in less than 20% of the older stands. What was not expected was the indication that species richness declined after the stands reached 60–70 years. One possible explanation is that the positive contribution of tree age is offset by corresponding decreases in other factors of importance for biodiversity, such as the presence of broadleaved trees (Felton et al., 2016c). This is supported by the fact that four of the five oldest stands had less than 1.5% of broadleaved tree species by basal area.

This suggests that in this forest type, the presence of broadleaved trees is more important than forest age for species diversity, and when the younger stands were excluded from the analyses there was a positive relation between the proportion of broadleaves and bird species richness. This is consistent with several previous studies which have highlighted the importance of deciduous trees and mixed forests for bird communities (Bibby et al., 1989; Forslund, 2003; Jansson and Andrén, 2003; Felton et al., 2011). Bird species richness may also have declined in the older forests due to a corresponding reduction in the diversity of tree size classes. The importance of structural complexity as a determinant of bird species diversity has also been shown to occur in many forest types (Hinsley et al., 2009; Hewson et al., 2011).

5. Conclusions

In summary, our study indicates that there is a range of potential adjustments to forest management that could be made that are likely to make measurable differences to the avian biodiversity found in these stands, and here we discuss three of these factors. First, we found that even a relatively small amount of broadleaves (often less than <15% of stand basal area) appears to be sufficient to have a positive effect on species richness. The FSC standard in Sweden now requires, where feasible, at least 10% broadleaved tree species by volume to be retained until the time of final felling within certified coniferous monocultures (FSC, 2010). Since at least 50% of productive forests in Sweden are FSC certified, our study shows that such an addition of broadleaved trees may be sufficient to elicit a positive response of bird species at stand level. As most coniferous production stands in southern Sweden have spontaneously regenerated broadleaves, if wanted, it would be fairly easy to increase the share of these species during pre-commercial and commercial thinnings. Second, our study also indicates the importance of tree age for the avian diversity. This could be increasingly relevant in the future as there are indications that rotation lengths are getting shorter in Sweden, as a consequence of a fear for climate associated risks such as storms and pest outbreaks (Felton et al., 2016a). Third, our study also indicates the beneficial influence of structural complexity on avian diversity, as indicated by the positive relation between the diversity of tree sizes and bird species richness. This means, that for the benefit of bird diversity, trees (and shrubs) of different sizes should be left during thinning and other management operations.

Although spruce production forests apparently do provide habitat for a number of bird species, it is important to consider the larger context of natural history and historical land-use in southern Sweden. Norway spruce is native to the region (Bradshaw and Lindbladh, 2005), but the current extent of high density and mono-specific stands of Norway spruce is unnatural, and primarily the product of intensive production forest management during the twentieth century (Lindbladh et al., 2014a). For this reason, the biodiversity contribution of spruce production forests needs to be weighed against the likely higher biodiversity contribution of other production forest alternatives available in the region. For example, any suggested benefits to the bird diversity from Norway spruce production forests are unlikely to be comparable to those provided by oak (Quercus spp.) (Felton et al., 2016b) or mixed spruce-birch production forests (Forslund, 2003; Felton et al., 2010b, 2016c).

Finally, we suggest that despite our findings, there continues to be a shortage in our understanding of which silvicultural measures would be sufficient to close the gap between the habitat requirements of avian conifer and broadleaved forest specialists, and the habitat provided in Norway spruce production. To identify the measures needed, and which birds would most likely benefit, will require comparisons with conifer-dominated natural forest systems in the region. Valuable insights have been derived from comparisons of managed forest with reserves in Finland (Forsman et al., 2013), Estonia (Rosenvald et al., 2011), and Norway (Haavik and Dale, 2012). We suggest that similar assessments are now needed in our region to provide further insights regarding how the habitats of spruce production forests can be improved.

6. Conflict of interests

The authors declare no conflict of interest.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.04.029.

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