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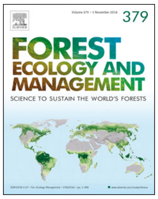

Comparing the effects of even-aged thinning and selective felling on boreal forest birds

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ABSTRACT

Biodiversity is in decline and therefore alternative forest management approaches have gained interest. One of such approaches is uneven-aged silviculture, which has been suggested to better maintain mature or late-successional forest characteristics and species assemblages than even-aged silviculture. Therefore, it is assumed that uneven-aged silviculture can be a useful tool for landscape planning to benefit biodiversity. Nevertheless, there is a lack of empirical studies regarding bird responses to uneven-aged silviculture in north European boreal ecosystems. Here we test the similarity of bird assemblage structure between mature forests within even-aged silviculture ('thinning') and uneven-aged silviculture ('selective felling'). In spring 2018 we censused breeding birds using territory mapping in 14 thinned stands and 14 selectively felled stands. We found higher abundance and different bird assemblages in thinned stands compared to selectively felled stands. The pied flycatcher, tree pipit and great tit contributed most to the variation of bird assemblages between the two management types. None of the species were more abundant in selectively felled than in thinned stands. According to functional guilds, the abundance of ground breeders, ground feeders and generalists was higher in thinned stands than in selectively felled stands, similar results were found in the species richness of long-distance migrants, ground nesters, secondary cavity nesters and generalists. Independent of management type, time since treatment had an overall effect on assemblage structures, the mistle thrush and wren were negatively correlated with time since treatment, while the chiffchaff showed the opposite trend. Our results suggest that at these locations and given this particular type of uneven-age management, selective felling is less suitable for some abundant generalists than even-aged forest stands reaching the thinning age. However, the results from this study does not provide clear management recommendations aiming to maintain biodiversity, as management guidelines should be based on red-listed species and not on common generalists. Nevertheless, our results stresses the urgent need for more long-term studies comparing the effect of these different silvicultural strategies on bird assemblages.

1. Introduction

Globally, biodiversity is in decline as a result of human-induced habitat loss, fragmentation and structural homogenization at multiple spatial scales (Vitousek et al. 1997, Butchart et al. 2010, Isbell et al. 2013). In the boreal biome, a widely adopted framework for counteracting negative impact of forest management on biodiversity is the natural disturbance emulation hypothesis (Pickett and White 1986, Attiwill 1994). It states that biodiversity is more likely to be conserved if management maintains key ecosystem components by mimicking the frequency, severity and extent of natural disturbances (Kuuluvainen and Grenfell 2012). For a long time, it has been argued that large-scale stand-replacing disturbances resulting in an even-aged stand structure (mostly high-intensity fires) is the main natural phenomenon for nearly all boreal forests (Zackrisson 1977), and hence that clearcutting is an appropriate method for emulating natural disturbances (Mielikäinen and Hynynen 2003). However, the ecological effects of clearcutting are different from that of wildfire (Swanson et al. 2011, Heikkala et al. 2016). Furthermore, forest dynamics in boreal forest were naturally driven also by a variety of other small scale disturbance agents (e.g. wind, pathogens, and insects) that maintained a more or less continuous forest cover with smaller gaps (Kuuluvainen 2009, Bergeron et al. 2014). This has triggered interest in uneven-aged silviculture which maintains a continuous forest cover and is often referred to as irregular forestry or continuous cover forestry. Uneven-aged silviculture can be implemented in various ways e.g. by varying the

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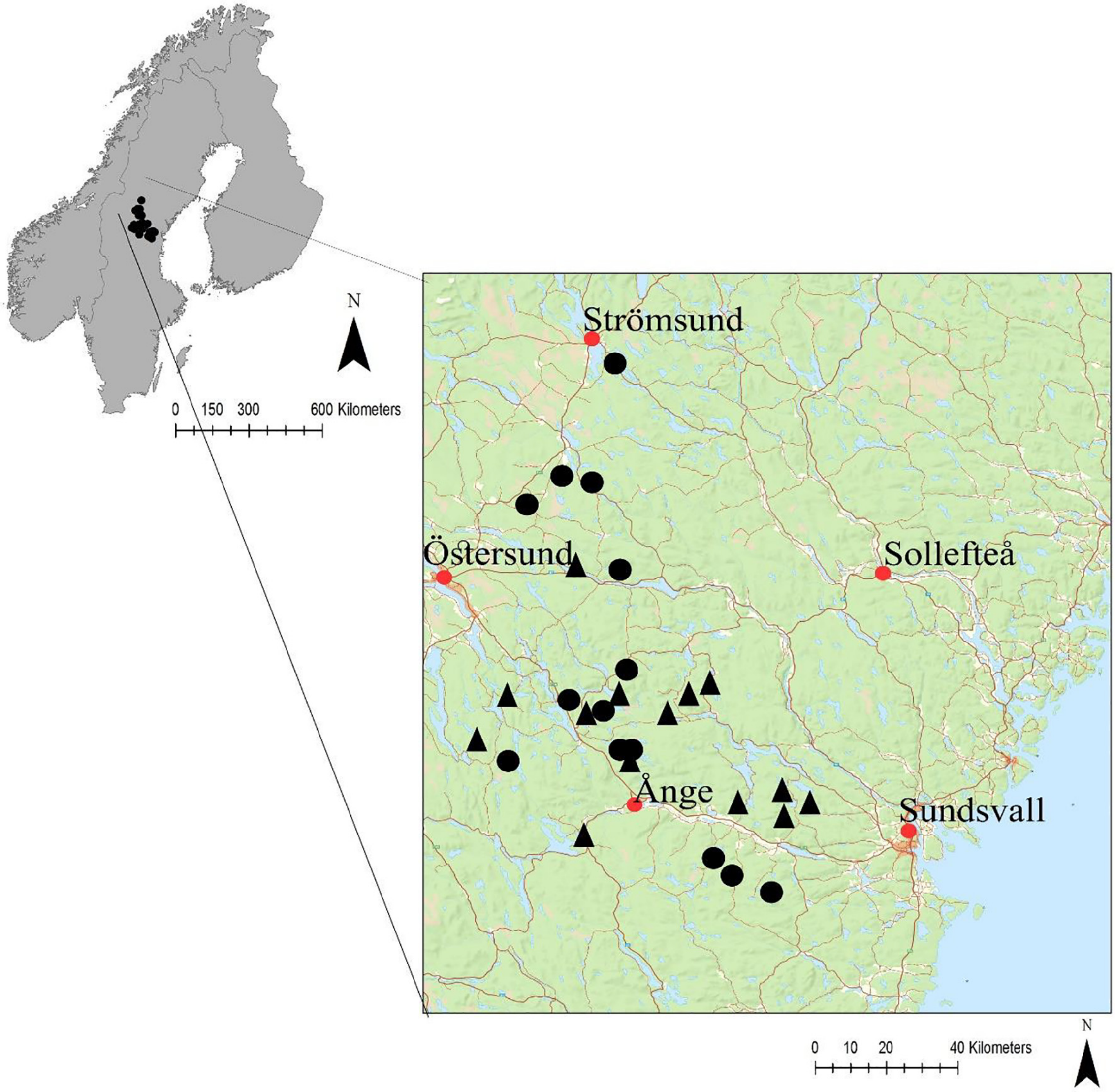

Fig. 1. Location of the experimental forest stands included in the study. Thinned stands (n = 14) are depicted with triangles and selectively felled stands (n = 14) with circles.

harvesting intensity along a gradient from single tree selection to patches or groups of trees of different sizes with gaps as large as 0.5 ha.

Uneven-aged silviculture better maintains mature or late-successional forest characteristics and species assemblages than even-aged silviculture (Koivula, 2002, Siira-Pietikäinen and Haimi, 2009, Kuuluvainen et al., 2012, Joelsson et al., 2017), which suggests that uneven-aged silviculture can be a useful tool for landscape planning to benefit biodiversity. However, a worldwide review by Nolet et al. (2018) showed variable effects of uneven-aged silviculture on biodiversity. Out of 99 cases used in this review, in 23 cases uneven-aged silviculture had a positive effect on species richness compared to even-aged silviculture, 16 cases showed the opposite, and 60 cases were equivocal. Thus current views that uneven-aged silviculture better maintains biological diversity and ecological processes than even-aged silviculture is not fully supported by the literature.

Most studies regarding this issue focus on forest structures, plants and invertebrates (Bagnaresi et al., 2002, Hjältén et al., 2017, Joelsson et al., 2017). Only a few studies have addressed the impact of uneven-aged silviculture on bird assemblage structures (Chambers et al., 1999, Thill and Koerth, 2005, Morris et al., 2013). Nolet et al. (2018) found 14 cases evaluating the responses in birds and found only one study that reported a positive effect. Nevertheless, we are not aware of any empirical study on bird responses to uneven-aged silviculture in north European boreal ecosystems, still, birds are potentially suitable for assessing the merits of uneven-aged forestry. First, their ecology is well known and the requirements of some species make them potentially useful as indicator species (Roberge and Angelstam, 2006, Pakkala et al., 2014, Versluijs et al., 2019) and umbrella species in conservation planning (Roberge et al., 2008, Bell et al., 2015). Second, boreal bird assemblages include many red-listed and declining species (Lindström and Green, 2015, Ram et al., 2017). Third, birds play key functional roles in forest ecosystems (e.g. tree cavity creation, invertebrate control, seed dispersal) (Pakkala et al., 2018).

In general, structural habitat diversity is positively correlated with species richness across taxonomic groups (Benton et al., 2003, Honnay et al., 2003, Lassau et al., 2005). In line, a long-term study from Finland, started in 1930, have shown that uneven-aged silviculture results in structural diverse forest habitats (Laiho et al., 2011). Thus it is expected that uneven-aged silviculture positively influences bird species closely associated with structurally complex habitats. By contrast, forest systems that have been simplified through even-aged silviculture are expected to provide poorer foraging opportunities for many bird species, as invertebrate prey are expected to be less abundant there than in more complex forest systems (Pettersson et al., 1995, Stenbacka et al., 2010). Moreover, complex forest habitats may provide diverse resources, nesting opportunities and protection from predators with the presence of deciduous trees, large diameter trees, a well-developed understory and high dead wood quantities (Tews et al., 2004, Gabriel et al., 2005, Herzon and O'Hara, 2007, Eggers et al., 2008). However, several studies have found that uneven-aged forests do not provide habitat for many migratory species requiring early-successional habitats (Thill and Koerth, 2005). It has therefore been suggested that with sufficiently long rotation lengths, even-aged silviculture can accommodate most forest birds by providing a complete spectrum of successional stages (Roberge et al., 2018). Within even-aged silviculture clearfelling will affect negatively bird species associated with old growth forests (Chambers et al., 1999, Thill and Koerth, 2005, Perry and Thill, 2013, Kellner et al., 2016), but the question remain if there are differences in bird assemblage structure between stands later in the rotation cycle of even-aged silviculture (from now on: 'thinning') and uneven-aged silviculture stands (from now on: 'selective felling'). The aim of this study is to assess the similarity of bird assemblage structure between thinned and selectively felled stands. We predict that selective felling enhances structural complexity in forest stands and will support a more species rich and diverse bird assemblages than thinned stands.

2. Methods

2.1. Study area and design

The study was carried out in the counties of Jämtland and Medelpad located in the boreal zone of central Sweden (63 °8′N – 62 °3′N and 15 °6′E – 16 °3′E, Fig. 1.). We collected data in 28 forest stands dominated by Norway spruce (*Picea abies*) (> 70%) mixed with birch (*Betula pendula* and *B. pubescens*), and smaller proportions of Scots pine (*Pinus sylvestris*), aspen (*Populus tremula*) and willow (*Salix spp*). Stand size varied between 2 and 21 ha, with an average size of 8 ha (Table 1.). Ground vegetation was dominated by bilberry (*Vaccinium myrtillus*). Thinned stands had been regenerated after clearcutting 40–60 years ago and have undergone commercial thinning with full timber extraction 2–23 years prior to the study. Selectively felled stands are mature forest stands with a mean tree age of 72 years (Table 1) originating from uneven-aged management, these stands have undergone selective felling 3–28 years prior to the study. In Sweden, the most used uneven-aged silviculture method is single tree selection felling, where single large-diameter trees are harvested. During selective felling approximately 30% of the standing volume was harvested. Harvest trails approximately 20 m apart were opened up during the initial harvest event and then trees were harvested by using the same harvest trails. The harvesters are only driven in the harvest trails, minimizing impacts on vegetation, forest recruitment and deadwood in the 20 m strips separating the machine corridors. The aim of selective felling was to maintain a stratified stand structure whereas the aim with thinning was to reduce tree size variation in the stands and reduce stem number. Both treatments are conducted with a standard harvester and forwarder. An illustration of typical stand structures can be found in supplementary material Figure S1. The stands were selected from a larger number (approximately 60) of candidate stands, based on stand data provided by the forest company SCA and visual inspection of all stands. To minimize between-stand variation, we standardized stand selection criteria but variation in stand characteristics still occurred between stands. Nevertheless, similar ranges were obtained within both stand types with respect to tree species composition [mix of pine (0–30%), spruce (60–90%), deciduous (5–20%)] and field layer vegetation (*Vaccinium myrtillus* or *V. myrtillus*–*V. vitis-idaea* dominated), mean tree age (Table 1).

Table 1
Overview of the 28 experimental stands. Mean ± SE is provided for stand variables. Management types were compared using a *t*-test, bold numbers highlight significant differences. Mean vegetation ratios derived from laser scanning data were used as proxy for canopy cover.

	Thinning	Selective felling	F	P-value
Number of stands	14	14		
Stand area (ha)	8.7 ± (0.9)	7.8 ± (1.2)	0.41	0.527
Time since treatment	11.8 ± (1.8)	10.3 ± (1.9)	0.58	0.566
Mean tree age (years)	51 ± (3.5)	72 ± (12.9)	1.41	0.171
Mean vegetation ratio (%)	69.1 ± (3.3)	57.9 ± (3.1)	1.99	0.065
Spruce %	79.9 ± (3.9)	79.5 ± (4.3)	0.04	0.966
Pine %	7.1 ± (2.6)	4.0 ± (1.7)	0.79	0.463
Deciduous	13.1 ± (3.1)	16.5 ± (3.5)	0.56	0.567

2.2. Bird censuses

In spring 2018, breeding birds in all study stands were censused through territory mapping (Bibby et al., 2000). Each study stand was visited 6 times from the beginning of April to the end of June. The time interval between subsequent visits was 12–15 days, depending on weather conditions. At each visit, all individuals displaying territorial behavior were recorded within the stand plus a 50-m buffer. Territorial individuals were determined through acoustic or visual cues (e.g. singing males, nests with eggs or nestlings, warning individuals). For data collection, a handheld tablet computer equipped with a Geographic Positioning System (GPS) and Geographic Information System (GIS) was used. This system gave access to maps and aerial photos of the study stands directly in the field. The position of each bird was determined based on the location of the observer, who was able to track his own position live on the digital map. In order to cover the whole territory mapping area in each study stand, the method was standardized by walking along fixed lines separated by 80 m, aiming for a predefined constant effort of 7.5 min of observation per hectare at all sites. Visits took place from half an hour before sunrise until seven hours after sunrise. In June, the starting time was fixed at 02:30 am. In case of heavy rain or strong winds, census work was cancelled and moved to the next day. The censuses were conducted by two experienced ornithologists. To minimize potential variation due to observer effects, each stand was visited 3 times by each of the two observers. The observers typically visited two paired stands in a single morning. Considering that the time of day may influence bird activity, the order of the stands visited within a morning (paired for logistical reasons) was shifted between visits.

Prior to statistical analyses of the bird data, observations from the 6 visits were clustered into territories for each species separately (Bibby et al. 2000). A territory was defined on the basis of a found nest and/or spatially restricted observations of territorial individuals recorded in at least two of the 6 visits (Bibby et al. 2000). Observations of birds in the 50 m buffer surrounding the study stands were included in the clustering of territories. Nevertheless, only territories with a minimum of 50% of the observations within the stand itself were considered as belonging to the stand (Berg 1997). All other territories were considered to be outside the study stand and were excluded from the analyses. See supporting information Table S1 for an overview of stand size, species richness and total abundance in each of the 28 stands.

2.3. Forest structure

Stand measurements were done in October 2018. Because the study sites varied greatly in size, sampling effort was standardized by placing 1 circular sampling plot per 2 ha, however restricting the number of plots to a maximum of five per study stand. The positions of the plots were randomized by selecting the points beforehand in ArcGIS. The following rules were applied in randomization: the plot centre must be at least 35 m from the edge of the stand, and each plots had to be at least 80 m apart. The point created in ArcGIS was marked as a plot centre in the field with a Trimble GeoXR 6000 differential GPS (Trimble

2013). The species, decay stage and diameter at breast height (DBH) of all living and standing dead trees ≥ 4 cm in DBH were measured within a radius of 10 m from the plot centre. In addition, in every second point all standing dead trees within a radius of 20 m were measured to get a better estimate of dead wood abundance. The undergrowth was measured from five systematically placed 1 m radius (3.14 m^2) plots by counting spruce trees over 1.5 m in height and with a DBH ≤ 4 cm. The counts of the 5 sampling plots per stand were pooled. For further analyses, data for all variables were averaged per study stand.

2.4. Landscape characteristics

Landscape variables were included in our models to correct for differences in local landscape characteristics. For that purpose, data were obtained on the total areas of (i) all forest older than 25 years (i.e. a measure of the cover of all forest excluding non-forested or very young forest areas in the regeneration phase) and (ii) older forest (> 70 years), which is expected to be important for old-growth forest specialists. These variables were obtained for radii of 1 and 5 km from the border of the study stands. Forest cover data were extracted from SLU forest maps (pixel resolution 25 × 25 m). SLU forest maps are derived from a combination of satellite imagery, field data, and algorithms that validate and determine k-Nearest Neighbor (kNN) distances in spectral space (Reese et al., 2003). Clearcutting data from the Swedish Forest Agency (Skogsstyrelsen, 2019) were used to update the SLU forest maps with clear-cuts created after 2010.

2.5. Statistical analysis

We used *t*-test to assess the similarity of forest structure between the two management types and among local landscape characteristics (i.e. forest older than 25 years and older forest (> 70 years), obtained for radii of 1 and 5 km from the border of the study stands). All bird species with observed territories in the study stands were included but owls (Strigiformes), diurnal birds of prey (Accipitriformes, Falconiformes), waders (Charadriiformes) and grouse (Galliformes) were excluded because (daytime) territory mapping is not an appropriate survey method to obtain estimates of their abundances. Similarity in bird species richness and abundance between management types was analyzed using generalized linear models (GLM) with Poisson error distribution. In the models evaluating effects on bird species richness, we included the logarithm of stand area as a covariate, to account for the relationship between stand size and species richness (Jonsson et al., 2011). Additionally, time of management is spread out over 30 years and therefore time since treatment was included as a covariate. There were no significant interactions between management type and stand area as well as with time since treatment in any of the models; therefore these interaction terms were omitted (supporting information Table S2a and S2b). In the models evaluating effects on bird abundance, the logarithm of stand area was included as an offset to control for the effect of stand size on the number of registered territories.

The same GLM structure as described above was used to analyses species richness and abundance within specific functional guilds. Species were assigned to migration guilds (short- and long-distance migrants, residents), foraging guilds (ground, crown and bark feeders), nesting guilds (ground nesters, off-ground nesters, strong cavity excavators (all of the woodpeckers observed in this study) and secondary cavity nesters (including weak excavators, i.e. willow tit, crested tit)) (Söderström 2009, Forsman et al. 2013, Wesołowski et al. 2015) and preferences for different successional stages of the forest vegetation (generalists, early-successional and mature forest) (Haapanen 1965, 1966, Imbeau et al. 2003) (See Supporting Information Table S3.

To explore the similarity of bird assemblage structure between management types, a multivariate generalized linear model with Poisson error distribution was used (ManyGLM; R-package “mvabund”, Wang et al. (2012)). ManyGLM uses the sum of log-likelihood from many individual GLMs to create a test statistic verified through randomization. This approach provides increased statistical power for detecting differences in communities of less abundant species that may be more poorly represented by distance-based approaches (Wang et al., 2012). Statistical significance was evaluated using 999 resampling iterations via ’Probability Integral Transform residual bootstrap (PIT-trap) resampling (Wang et al., 2012). Within the ManyGLM models we accounted for the effect of stand size on bird abundance by including the logarithm of stand area as an offset. Additionally, time since treatment was added to the model as well as the four landscape variables (i.e. forest older than 25 years and older forest (> 70 years), obtained for radii of 1 and 5 km). The significance of each variable was assessed with a likelihood ratio test and variables significantly affecting bird assemblages were included in the final model. The univariate test procedure, implemented in ManyGLM was used to test management type effects at the species level. To visualize ManyGLM outcome, we used a constrained redundancy analysis (RDA) within the R-package “vegan” (Oksanen et al., 2016). All statistical analyses were performed using statistical software R 3.3.1 (R Core Development Team, 2016).

3. Results

3.1. Forest structure

Basal area of living trees of each species separately (pine, spruce and deciduous trees), total basal area of living trees and density of living trees did not significantly differ between management types (Table 2). In contrast, the basal area of standing dead spruce, and basal area and density of dead trees, were higher in selectively felled than in thinned stands, whereas the DBH of living spruce trees showed the opposite. The DBH of living spruces were significantly smaller in selectively felled compared to thinned stands. The diameter distribution showed indeed a skewed distribution towards smaller diameter trees in selectively felled stands (See Supporting information Figure S2). Understory density was significantly higher in selectively felled than in thinned stands. The mean cover of forest older than 25 years or older than 70 years in the landscape neighborhoods of the study stands did not significantly differ between the two management types for any of the radii (Table 2).

3.2. Bird species richness and abundance

We found 702 territories of 30 bird species (all species pooled except the four excluded groups; see above). The two most abundant species were the common chaffinch (*Fringilla coelebs*) (175 territories) and goldcrest (*Regulus regulus*) (105 territories). Overall bird species richness did not significantly differ between management types (Table 3). In contrast, species richness of long-distance migrants, ground nesters and habitat generalists were significantly higher in thinned stands (Table 3). Furthermore, species richness of secondary cavity nesters was nearly significantly higher in thinned stands compared to selectively felled stands.

Total abundance of territories was nearly significantly higher in thinned stands (Table 3). Ground feeders, ground nesters and habitat generalists were significantly more abundant in thinned stands compared to selectively felled stands (Table 3). None of the landscape variables had a significant effect in any of the models presented in Table 3.

3.3. Species assemblage structure

The bird species assemblages differed significantly between the two management types (Fig. 2; Table 4). The assessed landscape variables did not have a significant effect on bird assemblage structures and were therefore not included in the model.

The univariate test procedure implemented in ManyGLM revealed that the pied flycatcher (*Ficedula hypoleuca*), tree pipit (*Anthus trivialis*)

Table 2
Tree stand structure (arithmetic mean SE) within the stands and in the landscape surrounding the stands (1 and 5 km radius). Management types were compared using a *t*-test.

		Thinning	Selective felling	T	P-value
Living trees					
DBH (cm)	Scots pine	22.6 ± (1.5)	26.3 ± (2.6)	−1.24	0.255
	Norway spruce	18.9 ± (0.8)	14.3 ± (0.7)	4.31	< **0.001**
	Deciduous trees	17.7 ± (1.3)	15.5 ± (1.5)	1.06	0.301
Basal area (m^2 ha^{-1})	Scots pine	1.7 ± (0.7)	1.2 ± (0.5)	0.63	0.537
	Norway spruce	22.2 ± (1.7)	21.6 ± (1.9)	0.24	0.809
	Deciduous trees	4.0 ± (0.9)	4.4 ± (1.1)	−0.25	0.802
Total tree basal area of living trees (m^2 ha^{-1})		27.9 ± (1.7)	27.2 ± (1.9)	0.31	0.763
Total density of living trees (ha^{-1})		950.6 ± (55.0)	1201.7 ± (118.3)	−1.92	0.071
Standing dead trees					
DBH (cm)	Scots pine	18.7 ± (1.9)	13.6 ± (1.9)	1.88	0.103
	Norway spruce	14.2 ± (1.4)	11.7 ± (0.9)	1.52	0.144
	Deciduous trees	13.0 ± (1.8)	10.8 ± (1.6)	0.89	0.389
Basal area (m^2 ha^{-1})	Scots pine	0.1 ± (0.04)	0.04 ± (0.03)	0.71	0.488
	Norway spruce	0.4 ± (0.1)	1.8 ± (0.6)	−2.31	**0.038**
	Deciduous trees	0.3 ± (0.1)	0.5 ± (0.2)	−0.84	0.416
Total tree basal area of dead trees (m^2 ha^{-1})		0.8 ± (0.2)	2.4 ± (1.6)	−2.21	**0.045**
Total density of standing dead trees (ha^{-1})		40.9 ± (8.1)	135.7 ± (27.8)	−3.28	**0.005**
Understory density					
Understory, number per 100 m2		18.4 ± (8.7)	69.6 ± (21.1)	−2.24	**0.039**
Forest cover in landscape neighborhood (ha)					
Radius 1 km	Forest > 25 years	191.8 ± (12.4)	188.0 ± (8.8)	−0.01	0.912
	Forest > 70 years	113.6 ± (10.4)	108.8 ± (11.8)	−0.12	0.761
Radius 5 km	Forest > 25 years	4596.3 ± (97.9)	4499.8 ± (117.0)	0.63	0.533
	Forest > 70 years	2281.3 ± (106.8)	2393.9 ± (145.7)	0.45	0.538

and great tit (*Parus* major) contributed most to the variation of bird assemblages between the two management types (Table 4). All these species were found in higher abundance in thinned stands. The interaction between time since treatment and management type was not significant, but time since treatment had an overall significant effect in the model. Species-specific results showed that the mistle thrush (*Turdus viscivorus*), wren (*Troglodytes troglodytes*) and chiffchaff (*Phylloscopus collybita*) were influenced by time since treatment. The mistle thrush and wren were negatively correlated with time since treatment, while the chiffchaff showed the opposite trend (Fig. 3, Table 4).

4. Discussion

As expected, selective felling enhanced variation within stand structures. However, our prediction that this would result in higher species richness of birds was not supported. To the contrary, we found similar total species richness between the two management types. At the guild level, thinned stands harbored higher species richness of long-distance migrants, ground nesters, secondary cavity nesters and generalists. In line with this finding, both total bird abundance and the abundance of ground breeders, ground feeders and generalists were higher in thinned than in selectively felled stands. Consequently, bird assemblage structures differed between the two management types. Thus, our findings do not support the hypothesis that selective felling favors bird species closely associated with structurally complex habitats.

4.1. Forest structures

As predicted, selective felling enhanced stand structures complexity when comparing it with thinning. Selective felling positively influences the basal area of dead Norway spruce, the quantity of standing dead trees and understory density of Norway spruce. In line with other studies, we found a smaller average DBH of the dominant spruce in

Table 3
Results of generalized linear models (GLMs) for bird species richness and abundance between two management types: Thinning (T) and Selective felling (SF). Models were fitted for the complete bird assemblage (“All species”) and separately for different guilds based on migration habits, foraging behavior, nesting sites and preference for forest successional stages. The raw data with means and variation of density (territories / ha) is provided in Fig. S3a, S3b and the guild classification can be find in Table S3.

		Species		Species richness				Abundance			
			Territories	Null dev“	Residual dev	P-value	Difference	Null dev“	Residual dev	P-value	Difference
	All species	30	702	34.6	20.8	0.108		51.9	38.8	0.053	
Guilds											
Migration	Resident	12	86	43.7	38.8	0.405		50.1	48.6	0.407	
	Short-distance	13	528	19.5	12.3	0.317		41.9	33.0	0.107	
	Long-distance	5	88	14.6	8.7	**0.029**	T > SF	37.1	31.2	0.236	
Foraging	Bark-feeders	4	33	21.8	20.4	0.360		27.1	26.2	0.369	
	Ground-feeders	13	399	25.9	15.9	0.158		45.1	34.3	**0.039**	T > SF
	Crown-feeders	19	494	21.9	13.3	0.205		37.7	30.8	0.150	
Nesting	Off-ground	15	511	19.6	12.3	0.451		37.1	31.6	0.102	
	Ground	3	61	15.8	12.7	**0.022**	T > SF	26.2	20.5	**0.017**	T > SF
	Strong cavity excavators	3	14	24.9	24.5	0.564		26.1	25.4	0.433	
	Secondary cavity nesters	9	116	24.9	19.1	0.053		38.4	31.9	0.110	
Successional status	Generalists	7	298	12.8	8.7	**0.028**	T > SF	25.7	17.3	**0.013**	T > SF
	Early-successional	4	54	26.6	20.1	0.869		34.2	33.3	0.349	
	Mature forest	19	350	21.9	15.8	0.124		30.5	25.0	0.249	

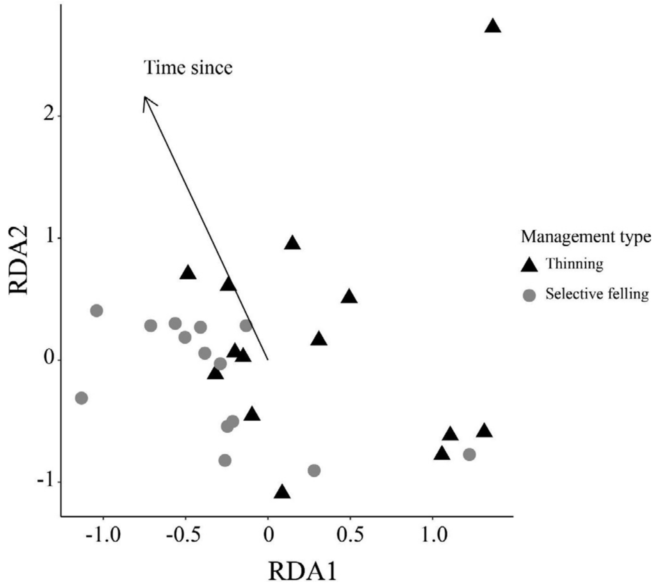

Fig. 2. Graphical representation of the constrained ordination redundancy analysis (RDA) of differences in species assemblage between the two management types. The vector represents the time since treatment.

selectively felled stands (Doyon et al., 2005, Laiho et al., 2011). Furthermore, the diameter class distribution was close to what is found in old-growth forests (Kuuluvainen et al., 2003). Thus, selective felling led to structural complex forest stands which structurally are more similar to old-growth forests then to stands subjected to thinning.

4.2. *Bird assemblage structure*

Both understory density and quantities of dead wood were better developed/higher in selectively felled than in thinned stands, which is assumed to result in greater species richness in boreal forest birds. Many birds benefit from a more developed understory and higher densities of dead wood (Eggers and Low, 2014, Virkkala, 2016, Ram et al., 2017). However, in this study we found the opposite, total bird abundance was nearly significantly higher in thinned stands than in selectively felled stands but significantly higher in ground feeders, ground nesters and habitat generalists. Furthermore, the pied flycatcher, tree pipit and great tit contributed most to the dissimilarity in bird assemblages between stands subjected to selective felling and thinning. The pied flycatcher and great tit are generalists but they tends to be more common in mature than in regenerating forests (Raivio and Haila, 1990). Additionally, both species are secondary-cavity nesters and therefore nest availability may be a limiting factor affecting their occurrence (Haapanen, 1966). In this study, densities of standing dead trees were higher in selectively felled stands and on average DBH was smaller than in thinned stands. This may result in less nesting opportunities for cavity nesters in selectively felled stands and consequently affect nest site availability for secondary cavity nesters. Ground nesters and generalists were more abundant in thinned stands than in selectively felled stands. Also the tree pipit, a habitat generalist but with a preference for early successional forest habitat, open forests and stand edges (Haapanen, 1966), was found in higher abundance. Changes in micro-climate (e.g. temperature and humidity), forest canopy cover, availability of large trees and increase in edge habitat are possible factors explaining the differences found in bird assemblage structure between management types. Additionally, these factors may affect insect densities (Hjältén et al., 2017, Joelsson et al., 2018), all affected bird species within this study are insectivorous. More research is needed for defining the factors behind the differences between the two management types, including sampling food availability.

4.3. *Time since treatment*

Independent of management type, time since treatment was a factor affecting bird assemblage structure. Although the response did not differ between treatments, overall species assemblage structure was affected by time since treatment. Early successional species and species closely connected to forest disturbances occurring in higher densities after harvest while species preferring structural layering increase over time (Morris et al., 2013, Perry and Thill, 2013). This is in line what we found in this study. For example, felling waste after harvest is expected to provide good breeding habitat for the wren (Kalela, 1938, Haapanen, 1965) and this type of habitat will disappear over time since harvest. Additionally, the mistle thrush prefers open conifer forest (Haapanen, 1965, 1966), created by harvest. As the stand becomes denser along succession, potential habitat for this species decreases, which should lead to lower abundance of this species, similarly as we found in our study. In line with our results, the opposite is expected to happen for the chiffchaff, they are expected to be positively influenced by succession, as they prefer structural complex forest systems with dense understory (Tiainen et al., 1983).

Table 4

Results of multivariate generalized linear models (ManyGLM) for the overall difference in species assemblage structure between the two management types: Thinning (T) and Selective felling (SF). Additionally, time since treatment was tested as continuous variable. The upper part of the table presents the multivariate test and the lower part presents the individual species responses for the 10 species contributing the most to the variation in bird assemblages. The raw data with means and variation of density (territories / ha) per species is provided in Fig. S4.

Multivariate test:						
Source	**DF**	**Dev**	**P-value**			
Time since treatment	1	51.77	0.032			
Management type	1	53.17	0.024			
Individual species response	**Time since**		**Management type**			
Species	**Dev**	**P-value**	**Dev**	**P-value**	**Difference**	**Contribution to variation (%)**
Pied flycatcher	5.25	0.062	8.22	**0.007**	T > SF	15.4
Tree pipit	3.63	0.057	7.10	**0.011**	T > SF	13.3
Great tit	0.01	0.947	4.78	**0.021**	T > SF	8.9
Siberian jay	0.32	0.529	4.23	0.052		7.9
Jay	1.29	0.356	3.97	0.080		7.4
Blackbird	0.09	0.779	3.57	0.092		6.7
Black woodpecker	0.09	0.712	3.11	0.137		5.8
Redwing	0.82	0.323	2.30	0.094		4.3
Coal tit	1.27	0.259	2.20	0.195		4.1
Crested tit	0.05	0.148	1.73	0.141		3.2

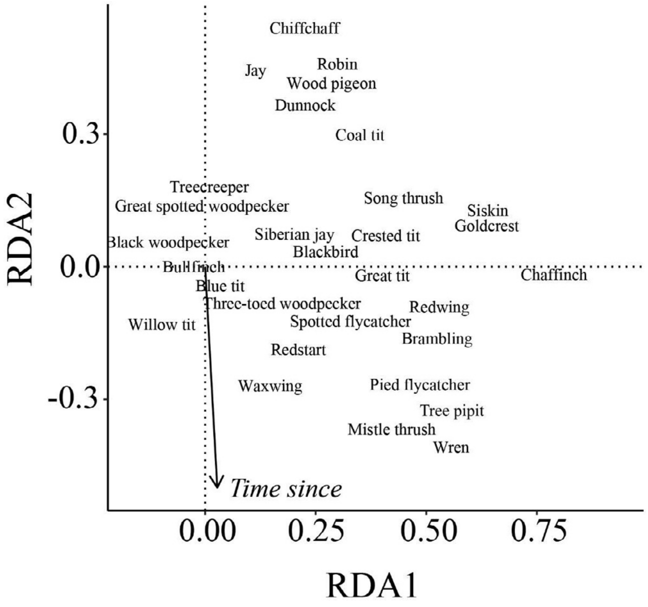

Fig. 3. Species scores obtained from a constrained RDA in relation to time since treatment.

4.4. Limitations of this study

Within this study, only one year of territory mapping data was collected, therefore we should be careful with the interpretation of the results. The one year of data does not account for annual variation in occurrences and densities of birds. Annual variation can be substantial in northern boreal forests (Haila et al., 1996). Nevertheless, we used relatively large sample size (n = 28) with distinguished assemblage structures and therefore we are confident that the reported patterns are most likely the effect of management. We have shown that management type influences forest structures and therefore it may potentially affect the detectability of birds (Gottschalk and Huettmann, 2011). For example, the more open structure of thinned stands may facilitate bird detection compared to selectively felled stands with denser understory cover. Estimates of bird densities in this study where obtained by the field-intensive territory mapping method, a method that minimize the potential risk of false absences linked to imperfect detectability. Additionally, this method does not seems to have a bird detection problem within this boreal forest environment (Versluijs et al., 2017) and therefore we assume that habitat complexity did not influence detectability and our results.

Another important aspect is that we only compared thinned stands with selectively felled stands. Within this experiment we left out a no-harvest control treatment and other stages in even-aged silviculture, e.g., the stage directly after clear-felling known to have profound effects on bird assemblages (Edenius and Elmberg, 1996, Rosenvald and Lõhmus, 2007). There is a bird community turnover during the secondary succession following clear-felling. Our study only covers the stages in the two silviculture systems most similar to each other from a management perspective. Selective felling aims to maintain complex stand structures and thinning (even-aged management) aims to reduce structural complexity. Thus our results are only indicative for the differences between these stages in the two silviculture systems.

4.5. Conclusion and management implications

This study suggests that selective felling is less suitable for some abundant generalists than even-aged forest stands reaching the thinning age. These common species are currently not listed as high-priority species from a conservation perspective but the pied flycatcher has declined significantly over the last two decades in Northern Sweden (Ram et al., 2017) and may therefore gain conservation interest in the future. In general, red-listed species and old growth specialist where rare in both management types despite the fact that selectively felled stands exhibit higher structural diversity. Our general findings contradict results for another group of organisms, saproxylic beetles, performed in the same study area and partly in the same study stands (Joelsson et al., 2017). This study shows that saproxylic beetle assemblages did not differ between selective felling and thinning. Differences in biodiversity found between even-aged management (i.e. clear-cutting and thinning) and uneven aged management are in general caused by early successional habitats created after clear-cutting (Chambers et al., 1999, du Bus de Warnaffe and Deconchat, 2008, Kellner et al., 2016, Joelsson et al., 2017). As uneven-aged forestry can be practiced in several different ways it should be made clear that our results are specific to the selective felling method used in this study and to our study region (Fennoscandia boreal forests). This also stresses the important to assess the effect of different uneven-aged management approaches on bird communities, preferably in long-term studies.

Our study stands mainly attracted common forest birds and rare bird species common in pristine forests (demanding exceptionally large trees, dead trees, etc.) were sparse in our data. This limits our ability to infer management recommendations based on our results. Nevertheless, for a boreal forest landscape to play a vital role for the conservation of biodiversity natural disturbance emulation should be applied as much as possible. This means providing a mixture of habitats of different successional stages, e.g., containing both early successional stages (partly produced by prescribed burning) and late successional forest (Rosenvald et al., 2011, Ram et al., 2017, Lindbladh et al., 2019).

CRediT authorship contribution statement

Martijn Versluijs: Methodology, Investigation, Formal analysis, Writing - original draft. **Anne-Maarit Hekkala:** Methodology, Investigation, Writing - review & editing. **Eva Lindberg:** Conceptualization, Methodology, Writing - review & editing. **Tomas Lämås:** Conceptualization, Methodology, Writing - review & editing. **Joakim Hjältén:** Supervision, Conceptualization, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118404.

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