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Short-term experimental support for bird diversity retention measures during thinning in European boreal forests

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ABSTRACT

Current levels of forestry expansion in boreal forests threaten to radically reduce biodiversity. For many forest-dwelling species the threat is not simply because the forest is used for biomass production, but rather how it is used. Retention forestry practices aim to limit impacts on biodiversity during the final felling stage of a forestry cycle. However, the efficiency of such methods in retaining biodiversity have rarely been studied for intermediate forestry stages (e.g., forest thinning) with experimental approaches entirely absent from boreal forests. Therefore, we conducted a before-after control-impact experiment in Sweden to investigate the short-term response in occurrence of individual bird species, guilds, and population trend groups (positive, stable, or negative population trend), as well as the response in nest box occupancy and in the reproductive success of *Parus major* to three different thinning treatments. The three treatments were i) conventional thinning at the plot and stand scale, (ii) understory retention thinning, where at least 250 spruces with live branches below 2 m above ground are retained per hectare, and (iii) complete retention plots, where the forest was not thinned on ~1 ha plots within conventionally thinned forest stands. We found that conventional forest thinning was likely the cause for observed declines in bird occurrence, with ~20% of the species showing clear negative responses. Our results indicate that understory retention thinning with double the retention level as previously suggested and combining conventional thinning with complete retention plots, could largely alleviate the short term negative effects of conventional thinning. This was the case for all guilds, population trend groups and individual bird species, except for *Poecile montanus*, which responded negatively to complete retention. Among the birds occupying the nest boxes, only *Cyanistes caeruleus* responded to any of the treatments, with higher nest box occupancy upon understory retention thinning. No thinning treatment affected reproductive success in *P. major*. Our results clearly show that thinning practices that retain the diversity of forest-dwelling birds are possible. Hence, this study provides a crucial puzzle piece towards more sustainable forestry practices in the boreal region.

1. Introduction

Current levels of forestry expansion will lead to an increased structural simplification of the boreal forest (Gauthier et al., 2015). In Fennoscandia, ~95% of the productive forest landscape has already undergone these changes (Angelstam and Kuuluvainen, 2004) with an accompanied strong decrease in biodiversity (Burton et al., 2010; Thompson et al., 2003). While the scarcity of many species in the boreal forest is due to replacement of natural with managed forests (Linder and Östlund, 1998; Tikkanen et al., 2006), many species are negatively affected by how these forests are managed and not because they are managed (Angelstam, 1998). Clear-cut rotation forestry is the dominating form of forest management in Fennoscandia. It is based on 80 – 100 years cycles with planting, one pre-commercial and up to three commercial thinnings during the intermediate stage with subsequent final felling (Esseen et al., 1997). Lately, research has revealed ways to minimise the often negative impact of clear-cut rotation forestry on biodiversity through different forms of green tree and dead wood retention during final harvesting (Gustafsson et al., 2010). However, there has been little focus on the effects of intermediate management stages (e.g. planting and thinning) and possible mitigation measures on biodiversity. This is unfortunate, because thinning greatly reduces the

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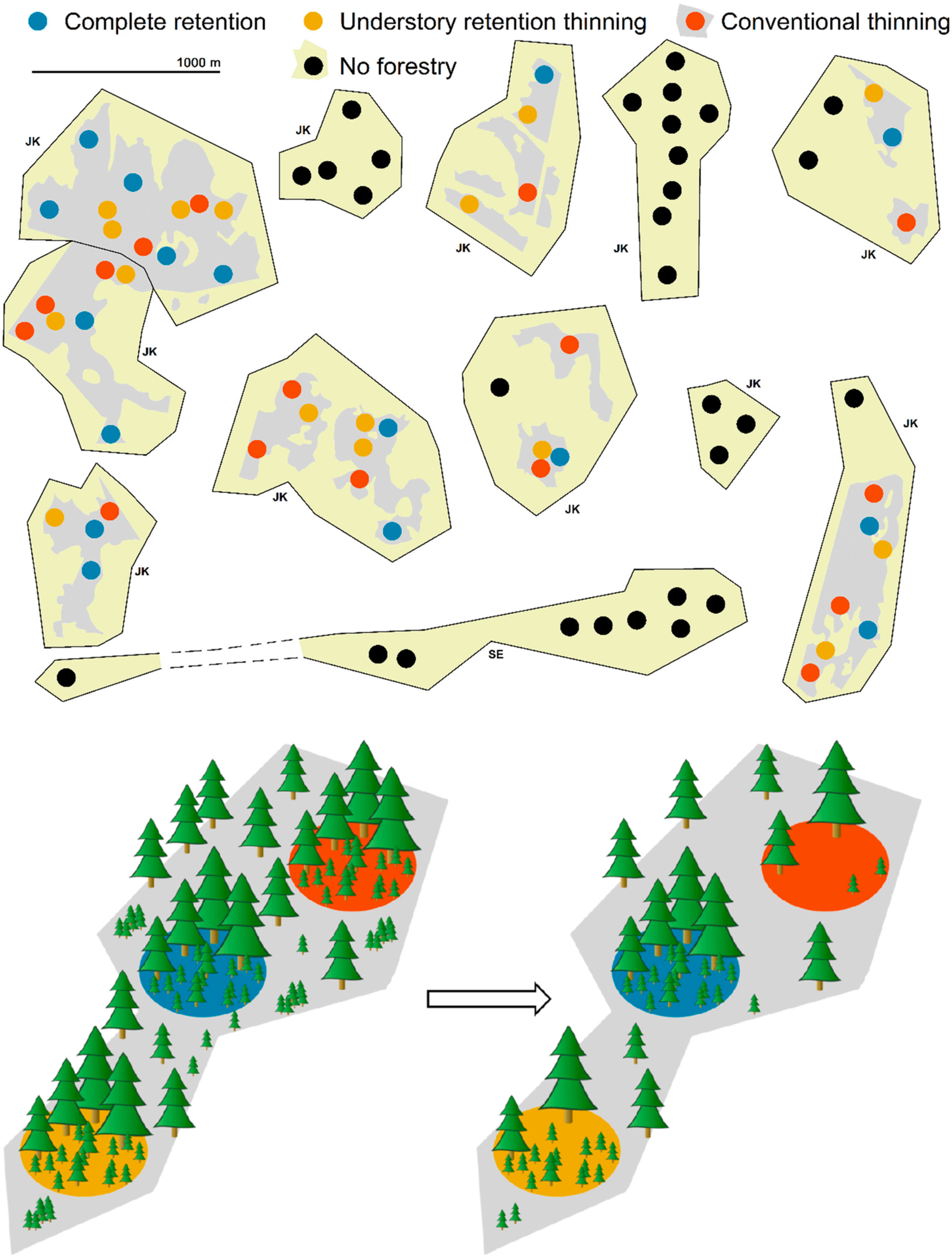

Fig. 1. Sketch of the experimental setup (top) and of a block with the three thinning treatments (bottom). The grey areas show the experimental forest stands. Stands within the same black polygon are included in the same block in the analysis. Within the experimental forest stands, we randomly chose 16 plots per thinning treatment (conventional thinning, understory retention, and complete retention), with at least one of each treatment in each stand. In addition to these 48 plots, 30 plots were assigned to stands in the surrounding landscape where no forestry occurred during the study period (illustrated by the light green colour in the figure). During the experiment, conventional forest thinning was performed on all of the grey areas as well as on conventional thinning plots. On complete retention plots, 100% of the vegetation was retained. On understory retention plots, at least 200 understory spruces were retained, but otherwise the plot was thinned conventionally. 'No forestry' plots were used as controls when we compared complete retention with conventional thinning and complete retention were used as controls when we compared understory retention to conventional thinning. We indicate which observer (JK or SE) performed the bird surveys in which block. The distances within blocks are actual, those between blocks are not. The dashed line means that the distance of the plots within this block was larger than indicated. The distance between any two plots ranged from 100 m to 20 km with 8.6 km in average. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

structural complexity in managed boreal forests over vast areas for long periods of time (Dodson et al., 2012) and thus most likely also affects biodiversity patterns at a large scale (Thompson et al., 2003; Verschuyl et al., 2011).

Birds are one group in which high species richness is usually a consequence of structurally complex forests (Müller et al., 2010). This is because structurally complex forests provide more protection during foraging (Griesser and Nystrand, 2009) and a greater variety of nesting opportunities (Chisholm and Leonard, 2008; Klein et al., 2020a). Conventional thinning homogenises tree stem diameter, the tree species composition (Klein et al., 2021), and reduces the basal area by 40 – 60% (Agestam, 2009). It further reduces vegetation density mainly in the understory (Ares et al., 2010; Homyack et al., 2004), where the complexity in the foliage layer is often crucial for bird diversity in boreal forests (Klein et al., 2020b; Lindberg et al., 2015). An alternative thinning method that retains parts of the understory foliage has therefore been suggested for Fennoscandia (understory retention thinning; Eggers and Low, 2014). In this method, as a singular contrast to conventional thinning, at least 250 Norway spruces (*Picea abies* (L.) Karst.) with live branches below 2 m above ground, are retained per hectare. Another measure to maintain structural complexity, which is used during final felling (Gustafsson et al., 2012), is complete retention patches, where the forest is not thinned on small islands within thinned forest stands. However, the effect of these retention methods as well as the effect of conventional thinning on bird diversity in managed boreal forests can until now be derived only from correlative studies (Eggers and Low, 2014; Klein et al., 2020b; Versluijs et al., 2020). While a denser understory, preserved through understory retention thinning or complete retention plots, is expected to lead to a higher species richness of forest-dwelling birds (Klein et al., 2020b; Lindberg et al., 2015), it is by no means clear whether different bird species, guilds or population trend groups are equally affected. Even if the number of species increases, it is unclear whether a change in the composition of forest structural elements (i) will have similar or opposing effects on different nesting and foraging guilds (Versluijs et al., 2017), (ii) contribute to the population decline of one bird group while not affecting another (Eggers and Low, 2014), or (iii) impact a single species disproportionally (Klein et al., 2020a). Powerful experimental approaches that can expose such processes, and that go beyond the evaluation of simple species richness metrics have not been performed in relation to conventional forest thinning and retention methods in the boreal region.

In this study we therefore experimentally test the effect of (i) conventional thinning without a specific understory retention measure, (ii) understory retention thinning, and (iii) complete retention plots within thinned stands, on the bird community in a managed boreal forest in Sweden. We do this using a two-level before-after control-impact (BACI) design. At level one, bird community impacts of conventional thinning and complete retention are evaluated against forest stands where no thinning occurs (Hereafter 'no forestry'). At level two, conventional thinning and understory retention are evaluated against complete retention. This design allows us to test two retention measures simultaneously and evaluate whether the effects of conventional thinning on birds are scale dependent (plot vs stand scale). To evaluate the treatments' impact on the bird community, we apply a recently presented method where readily interpretable indicators help determine whether changes during BACI experiments are causally related to the tested treatment. These indicators are based on whether impact and control plots were more similar before (good impact and control match) or after (bad match) the experiment (Box 1; Chevalier et al., 2019). Our objective is to (i) see if and how the occurrence of bird guilds (nesting and foraging behaviour, food consumption, habitat requirements), long term population trend groups (positive, stable, or negative), and of individual bird species, as well as nest box occupancy and the reproductive success of *Parus major* are affected by conventional thinning and (ii) whether possible effects of conventional thinning are larger at the plot or stand scale, (iii) to see if understory retention or complete retention can mediate possible negative effects of conventional thinning on the bird community, (iv) to test whether certain species react particularly to conventional thinning and retention measures, and (v) whether redlisted species are among them.

2. Material and methods

2.1. Study area and thinning experiment

The study area is located in central Sweden east of Uppsala (59.84° N, 17.96° E). The forest in this region is dominated by Norway spruce (*Picea abies* L. Karst.) and Scot's pine (*Pinus sylvestris* L.), while deciduous trees, predominantly birch (*Betula* spp.) and aspen (*Populus tremula* L.) are rarer. A forestry company (Holmen AB) provided us access to eight forest stands totalling 250 ha, and also thinned the forests according to our experimental design in the winters (October – February) of 2017/18 and 2018/2019. The stands were 40 to 70 years old and contained forests with differing degrees of structural complexity; these were representative of managed forests subject to commercial thinning in the boreal region of Fennoscandia. From the candidate set of 117 plots with a radius of 50 m (0.79 ha) that could be placed in the eight forest stands, excluding bogs, lakes and forestry roads, we randomly selected 48 experimental plots and then randomly assigned the plots to one of the three impact treatments (conventional thinning, understory retention, and complete retention) with 16 plots per treatment and at least one of each treatment per forest stand (Fig. 1). Conventional thinning was performed on the whole area of the experimental stands except on the understory retention and complete retention plots; thus after thinning, understory retention and complete retention plots were islands within a conventionally thinned landscape (Fig. 1). To ensure a correct implementation of the treatments by the foresters, we marked the borders of conventional thinning and complete retention plots and the 200 (250/ha * 0.79 ha) understory spruces on understory retention plots in the field. Spread across the study area, we placed an additional 30 plots where no forestry at all occurs in the plots' vicinity during the course of the experiment ('no forestry'). We then used these 'no forestry' plots as controls when comparing the effects of conventional thinning and complete retention plots on the bird community. To evaluate how effective understory retention is as a biodiversity retention measure, we compared understory retention to conventional thinning and used complete retention plots as controls. We regard complete retention plots as suitable controls in this context, since no thinning occurs on complete retention plots and the surroundings of conventional thinning, understory retention, and complete retention plots are equally affected by forest thinning (See Fig. 1 for the spatial arrangement of the experiment). 'No forestry' plots were placed both within and outside of experimental blocks, which means that they were situated in managed forests similar to the impact plots as well as in protected nature reserves. We also chose nature reserves, because we wanted to ensure that some 'no forestry' plots remain unaffected during the next 20 years to allow long-term assessments of this experiment. We expected the bird community in 'no forestry' plots to be comparable to the pre-treatment conditions on the experimental stands as they lay within the same forest region. We tested whether this was the case, namely whether the occurrences of all bird species differed between 'no forestry' plots and experimental plots before the experiment.

2.2. Data collection

2.2.1. Bird species occurrence

During each plot visit, we noted the occurrence of all bird species heard or seen within 50 m (estimated with preceding distance estimation training) from the plot centre (except flyby birds) during two five-minute sessions (20 min apart in 2017 and 5 min apart in 2018 and 2019). We reduced the time between surveys in 2018 based on data collected 2017 that showed species were consistently observed within the first 15 min of an observer's arrival at a plot (Appendix: Table A.1). Each plot was visited between 30 min before and six hours after sunrise (with the order of visitation varied between surveys), between three and five times from April 1st to June 21st. All 78 (48 experimental + 30 no forestry) plots were surveyed in 2017 and 2018. In 2019 only the plots where thinning had occurred during winter 2018/2019 as well as the associated 'no forestry' plots were surveyed. The same observer (JK or SE) always visited any given plot. Because of different arrival times of migrating birds into the study region, long-distance migrants were present during fewer plot visits than short-distance migrants or resident species (3 to 4 visits versus 5 on the 69 plots surveyed by JK and 1 to 3 versus 2 to 5 on the 9 'no forestry' plots surveyed by SE; Fig. 1). We did not include the following bird species in the data because their presence or absence on a plot is assumed coincidental or very unlikely associated with the forest structure on the experimental plots: *Fringilla montifringilla* and *Acanthis flammea* because they do not breed in the study region, *Loxia* spp. because they do not breed during the survey period, *Carduelis spinus* because they breed in colonies in the vicinity of spruce cone mast events, and raptors, owls, corvids, grouses, woodpeckers, doves, *Cuculus canorus*, and *Scolopax rusticola* because they have home ranges clearly larger than the size of the experimental plots (von Blotzheim, Urs N. Glutz Bauer and Bezzel, 1994). Using peer-reviewed scientific literature on bird traits, we grouped all bird species into different guilds (nesting: ground-, canopy-, or hole-nester; foraging: ground-, canopy-, or bark-feeder; food: insectivore or omnivore; habitat requirement: structurally trivial, structurally complex, or deciduous forest; Ottwall et al., 2009; Forsman et al., 2010; Wesołowski et al., 2015) and whether a species in Sweden has an increasing, decreasing or stable population trend (Appendix: Table A.2; Lindström, 2017).

2.2.2. Nest boxes

To evaluate the effect of the different thinning treatments on nest box occupancy and reproductive output of *P. major*, in the winter of 2016/2017, we placed two nest boxes (5 cm opening) in each plot; 25 m to the east and to the west of the plot centre, respectively. The nest boxes were nailed to a tree 1.5 m above ground, facing southeast. During spring, we checked the nest boxes every 5–10 days for the occupying species, number of eggs, hatchlings, and fledglings. We defined a nest box as occupied by a species when at least one egg was laid. If the species occupying the nest box could not be determined or if the number of occupancies across all plots per species was too low for model fitting (≤ 5), the nest box was excluded. In case a *P. major* occupied a nest box, we considered the number of nestlings aged 10 days or older as the reproductive output of this nest.

2.2.3. Forest structure

We collected data related to local forest structure within a 10 m radius subplot located at both nest boxes and the plot centre on every plot. We did this to compare the forest structure between the different treatments before and after the experiment as well as the changes on impact plots. On every subplot, we measured the diameter at breast height (DBH) and noted the species of every tree with a DBH > 5 cm and whether it was alive. We also counted all spruce trees (regardless of DBH) that contributed to a dense understory (live branches down to below 2 m above ground). Additionally, as a proxy for forest structural complexity, we measured the visibility distance in the forest by means of a laser device (Leica DISTO™ A5). This was done by measuring the distance from the centre of the plot to the first intersecting tree stem or branch at every 30°horizontally and at a 45-degree upward angle, resulting in 24 measurements per plot.

2.3. Statistical analysis

2.3.1. Bird species occurrence

We used a multi species occupancy model (MSOM), a standard method which estimates a species' true occurrence on a plot by incorporating detection probability (Royle et al., 2005), to investigate the effect of the three different thinning treatments on the bird community. We used the detection frequency across all survey periods per plot, year and species as the response and modelled this frequency using a binomial distribution with the true occurrence multiplied by the detection probability and the number of survey sessions as the distribution parameters. For each bird species we then estimated the probability of occurrence on conventional thinning, understory retention, complete retention, and 'no forestry' plots both before (spring 2017) and after (spring 2018 or 2019) the experiment (4 treatments * before/after = 8 intercepts for every bird species), while accounting for the effect of the year of observation, using a Bernoulli-GLMM with the experimental block as the grouping factor. We used the experimental block as a grouping factor to account for possible landscape effects on bird occurrence irrespective the experimental treatment. We did not include landscape covariates because we assume that they remain unchanged during the three years of the experiment. We estimated the species level detection probability, while accounting for the observer and the year of observation due to yearly changes in abundance, using a logit function. We added an observation level random effect due to over-dispersion in the data (Harrison, 2014). MSOMs are typically implemented in a Bayesian framework where the species-specific parameter priors are assigned a community hyperprior to use information from common species for the parameter estimates of rare species (i.e. Bayesian shrinkage; Iknayan et al., 2014). For these we used a vague Normal hyperprior for the mean and a Half-Cauchy hyperprior (Gelman et al., 2008) for the standard deviation of the parameter priors' Normal distribution. To implement the MSOM and to generate Markov chain Monte Carlo (MCMC) based posterior distributions of the parameters, we used JAGS (Plummer, 2003) and the packages *rjags* (Plummer, 2019), *coda* (Plummer et al., 2006) and *runjags* (Denwood, 2016) in R (R Development Core Team, 2020). We calculated the posterior distributions with three different initial chains, with a burn-in of 100,000 and with subsequent sampling of every 500th iteration until a total sample size of 1000 per chain was reached. We assumed chain convergence when the potential scale reduction factor was below 1.1 (Gelman and Rubin, 1992) and tested how well the model predicts the mean, the coefficient of variation, and the residuals of the original data (posterior predictive checks; Hooten et al., 2015). The whole analysis can be found on https://doi.org/10.5281/zenodo.5970855.

To compare conventional thinning with complete retention ('no forestry' as control) as well as conventional thinning with understory retention (complete retention as control), we then calculated for all thinning treatments the Bayesian posterior probability of the BACI indicators (Box 1) being positive or negative for all species, guilds and population trend groups according to Chevalier et al. (2019) and

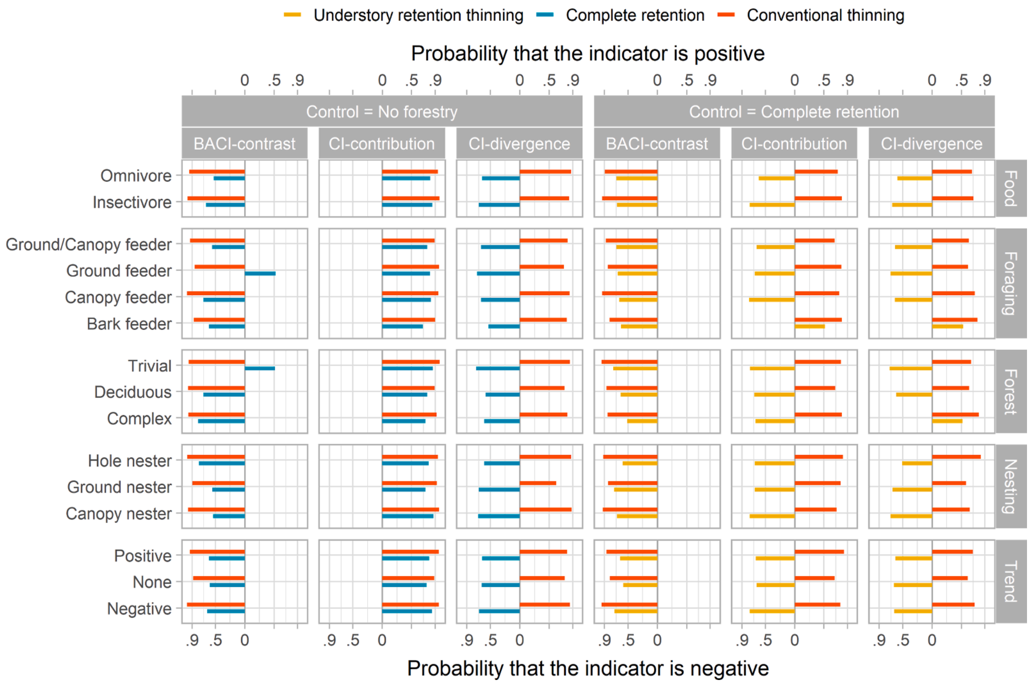

Fig. 2. For the average plot occurrence of guilds and population trend groups, we here show the Bayesian posterior probability of a BACI indicator being positive (if P (positive) > 0.5 then the bar is on the right side of the zero line) or negative (if P(negative) > 0.5 then the bar on the left side of the zero line) for all treatment comparisons. Consult Box 1 to interpret the BACI indicators.

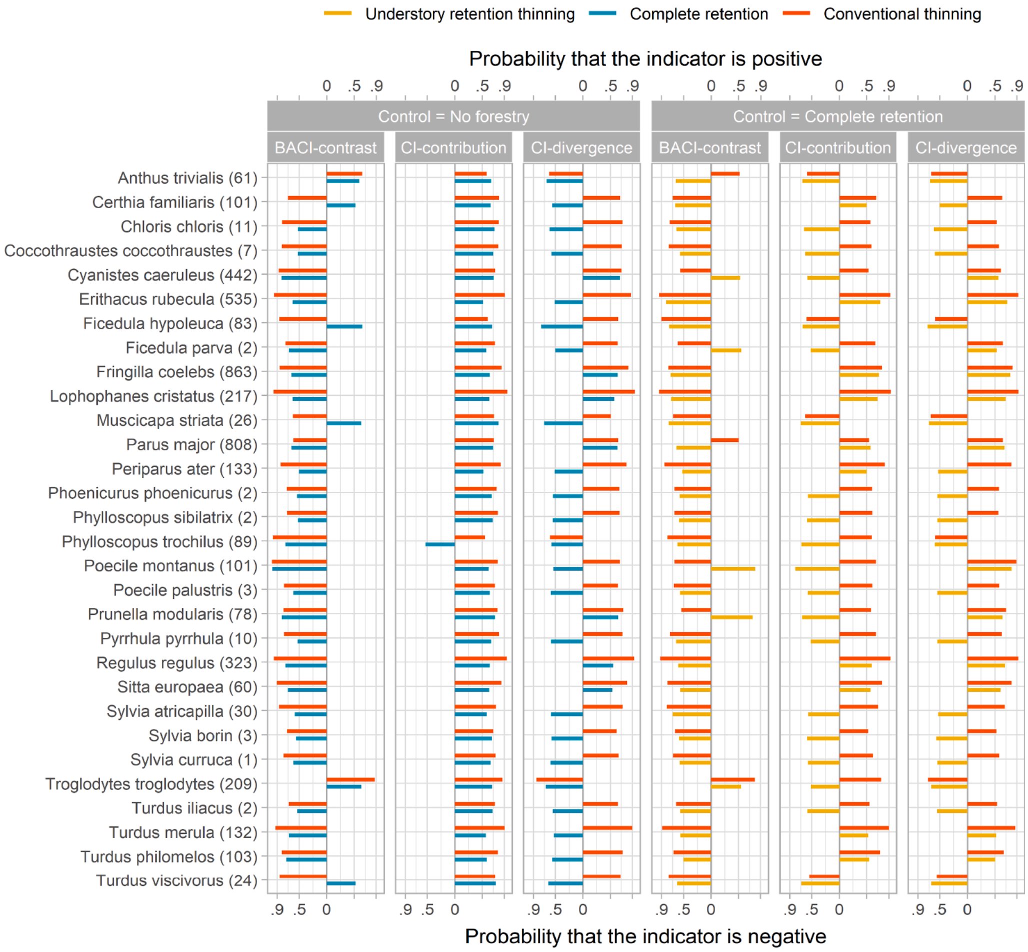

Fig. 3. For the occurrence of every bird species, we here show the Bayesian posterior probability of a BACI indicator being positive (if P(positive) > 0.5 then the bar is on the right side of the zero line) or negative (if P(negative) > 0.5 then the bar on the left side of the zero line) for all treatment comparisons. Consult Box 1 to interpret the BACI indicators. The number of occurrences throughout the study periods are given as a further help in interpreting the probabilities. Species red-listed in Sweden are Chloris chloris (EN), Ficedula hypoleuca (NT), Phylloscopus sibilatrix (NT), Poecile montanus (NT), Poecile palustris (NT), Sylvia curruca (NT), and Turdus iliacus (NT) (SLU Artdatabanken, 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

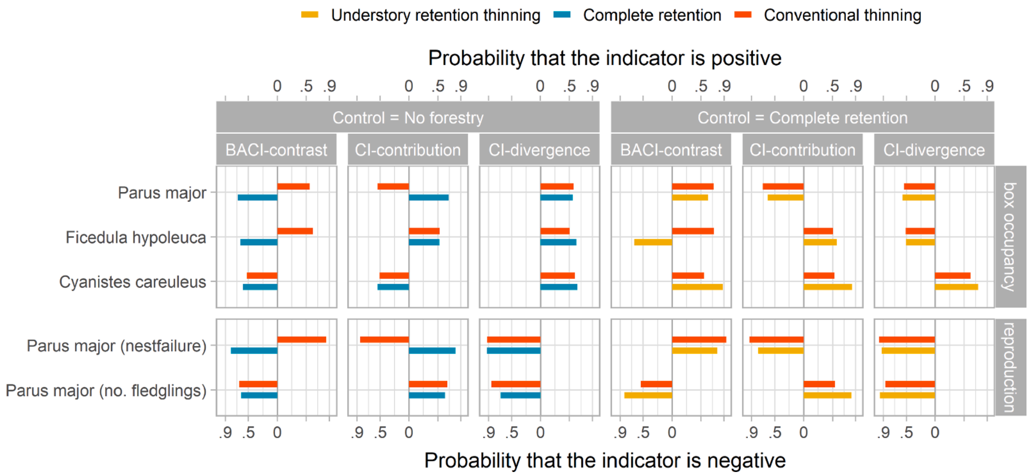

Fig. 4. For nest box occupancy and reproductive success of P. major, we here show the Bayesian posterior probability of a BACI indicator being positive (if P (positive) > 0.5 then the bar is on the right side of the zero line) or negative (if P(negative) > 0.5 then the bar on the left side of the zero line) for all treatment comparisons. Consult Box 1 to interpret the BACI indicators.

visualised the results with *ggplot* (Wickham, 2011). We also compared the probability of occurrence of all bird species between ‘no forestry’ and thinning plots (conventional thinning, understory retention, and complete retention) to see if original conditions were comparable from the bird’s perspective.

Box 1: The BACI indicators explained.We used a set of novel indicators by Chevalier et al. (2019) to determine to what extent a change in occurrence of forest birds and bird guilds can be attributed to the thinning treatments. These indicators are especially useful when graphical evaluations are unfeasible, such as in this study where a high number of species are evaluated and compared at once. The before-after control-impact contrast (BACI-contrast) is a frequently used evaluation metric in experimental studies and tells whether an observed change on impact plots is directionally different to the observed change on control plots. However, Underwood (1997) states that an observed change on impact plots can only be attributed to the impact treatment with certainty, if the magnitude of change is larger on impact than control plots (CI-contribution). Chevalier et al. (2019) further suggest an indicator measuring the magnitude of divergence between impact and control plots during the course of an experiment (CI-divergence). If a BACI-contrast is non-zero, CI-divergence reveals how similar (positive values) or dissimilar (negative values) control and impact plots were before the experiment, and thereby expose whether impact and control plots were a good match. Therefore, only a non-zero BACI-contrast together with positive CI-contribution and CI-divergence values fulfils Underwood’s criteria for a causal relationship between an observed change in the response and the impact treatment (Chevalier et al., 2019; Underwood, 1997).

Abbreviation	Calculation	Explanation
BACI-contrast	= (ImpactAfter – ImpactBefore) - (CotrolAfter – ControlBefore)	The BACI-contrast measures whether an observed change on the impact plot was more positive or more negative compared to the change on a control plot.
CI-contribution	= |ImpactAfter – ImpactBefore| - |ControlAfter – ControlBefore|	If the BACI-contrast is non-zero, CI-contribution tells whether the observed BACI-contrast was mainly due to a change on the impact plot (positive) or the control plot (negative).
CI-divergence	= |ImpactAfter – ControlAfter| - |ImpactBefore – ControlBefore|	If the BACI-contrast is non-zero, CI-divergence tells whether the control and impact plots were more similar before (positive) or after (negative) the experiment.

Interpreting an example from Fig. 3 for *Phylloscopus trochilus* in the evaluation of conventional thinning with ‘no forestry’ as the control:*P. trochilus* shows a clear negative ($P \geq 0.9$) response to conventional thinning (negative BACI-contrast), but this negative response is due to a change in *P. trochilus* occurrence on both conventional thinning and ‘no forestry’ plots (neutral ($P \approx 0.5$) CI-contribution). The probability of occurrence of *P. trochilus* on conventional thinning and on ‘no forestry’ was equally dissimilar after compared to before the experiment (neutral CI-

(*continued on next column*)

(*continued*)

divergence for conventional thinning). Because the BACI-contrast for conventional thinning was negative, this neutral CI-divergence means that *P. trochilus* occurred with a higher probability on conventional thinning than on ‘no forestry’ plots before the experiment and vice versa after the experiment. Concluding; the negative response of *P. trochilus* to conventional thinning cannot with certainty be attributed to this treatment and impact (conventional thinning) and control (‘no forestry’) plots were not an ideal match for this species.

2.3.2. *Nest boxes*

To find out if the different thinning treatments affected which bird species occupied a nest box, we used a Multinomial logistic model with the possible occupying species plus *empty* as the response categories. For the number of fledglings, we use a zero inflated Poisson model, where a Bernoulli process defines whether a nest failed, and the Poisson process how many birds fledged, given the nest was successful. As in the model for bird species occurrence, we used the eight intercepts (4 treatments * before/after) and the year effect as explanatory variables in all models. From these intercepts we then calculated the probability of the BACI indicators being positive or negative for all treatment comparisons and the three responses, box occupant, nest failure, and number of fledglings in successful nests. We implemented both models in a Bayesian framework with the same tools as in the section *bird species occurrence* above using vague Normal priors. In addition to posterior predictive checks, we calculated Moran’s I in both models to see if the data from neighbouring nest boxes was spatially independent. The whole analysis can be found on https://doi.org/10.5281/zenodo.5970855..

2.3.3. *Forest structure*

To compare the categorical means of all forest metrics between the different treatments before and after the experiment, we used simple Gaussian linear regressions and visualised the results with *ggplot*. Normality of residues and homoscedasticity were inspected visually. We calculated the total basal area (BA, m^2/ha) from the average plot DBH multiplied with the number of trees, and then which percentage of the BA could be attributed to Scot’s pine, Norway spruce, deciduous trees and standing dead wood. For the visibility metric, we calculated the mean measurable distance, with assigning the maximum measurable distance on a plot to measurements where the laser beam was not reflected. Additional metrics were the number of understory spruces, tree species richness and the coefficient of variation of the tree DBH.

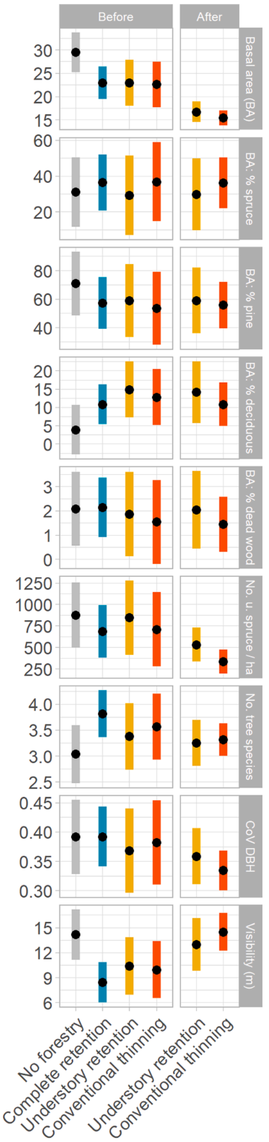

Fig. 5. We used linear models to compare all treatments before and after (Only conventional thinning and understory retention) the experiment according to several metrics that measure forest structure. The mean and 95% Confidence intervals are shown.

3. Results

3.1. Bird species occurrence

3.1.1. Guilds and population trend groups

Conventional thinning had a negative effect (negative BACI-contrast) on almost all guilds and population trend groups (Fig. 2). This negative effect was, according to Underwood’s (1997) criteria for experimentally exposing causality, likely the direct result of the conventional thinning treatment, because the change in occurrence was stronger (positive CI-contribution) on conventional thinning than on control plots (complete retention or ‘no forestry’), and because occurrence on thinning and control plots was more different after than before the experiment (positive CI-divergence; Fig. 2, Box 1). The negative effect of conventional thinning was stronger and causality more likely when ‘no forestry’ rather than complete retention was used as the control (Figs. 2 & 3), indicating that the bird community was more strongly affected by conventional thinning at the stand than at the plot level. Complete retention and understory retention had only weak or no effects with non-positive associated BACI-indicators (Fig. 2).

3.1.2. Bird species

Many of the 30 bird species showed a weak or no response to the thinning treatments (Fig. 3). However, *Sitta europaea, Turdus merula, Lophophanes cristatus, Regulus regulus,* and *Erithacus rubecula* responded negatively to conventional thinning but not to complete retention when ‘no forestry’ was the control and *L. cristatus, R. regulus,* and *E. rubecula* also responded negatively to conventional thinning but not understory retention when complete retention was the control. All of these effects were likely causal (positive CI-contribution) and the matching of control and impact plots was appropriate (positive CI-divergence). *Phylloscopus trochilus* and *Poecile montanus* are species that reacted negatively to conventional thinning when ‘no forestry’ was the control but neither to conventional thinning nor understory retention when complete retention was the control (Fig. 3). For both species, neutral CI-contribution values for conventional thinning with ‘no forestry’ as the control indicate that the negative effect of conventional thinning at the stand level cannot with certainty be attributed this treatment. Also, the negative BACI-contrast together with the neutral CI-divergence values for conventional thinning with ‘no forestry’ as the control indicate that the occurrence of *P. trochilus and P. montanus* was higher on conventional thinning than on ‘no forestry’ before the experiment and vice versa after. Thinning and control plots were therefore not an ideal match for these species. It was also only *P. montanus* and *P. trochilus* that had a different (lower) probability of occurrence on ‘no forestry’ compared to all thinning plots before thinning (Appendix: Table A.3). *P. montanus* was the only species that reacted clearly negatively to complete retention but with neutral CI-contribution and CI-divergence values (Fig. 3). It was also the only red-listed species that responded to any of the thinning treatments. *Troglodytes troglodytes* was the only species which showed a weakly positive response to conventional thinning with both controls, but the causality of this relationship is uncertain (Fig. 3).

3.2. Nest boxes

P. major, *Ficedula hypoleuca,* and *Cyanistes careuleus* were the only species that occupied more than five nest boxes. Understory retention had a positive effect on the occupancy probability of *C. careuleus* (Fig. 4). No other treatment had any effect on the occupancy probability of any species. Conventional thinning at the plot level increased nest failure in *P. major*, however with negative CI-indicators, suggesting bad treatment matching and a stronger change on control than on impact plots (Fig. 4).

3.3. Forest structure

The forest measurements before the experiment were similar (95% CIs of one category overlaps with the mean of another category) among all thinning plots (conventional thinning, understory retention, complete retention) but lower compared to ‘no forestry’ plots in their total basal area (BA), percentage pine, and visibility, and higher compared to ‘no forestry’ plots in their percentage deciduous and tree species richness (Fig. 5). After thinning, conventional thinning plots and understory retention plots only differed in the number of understory spruces per hectare; understory retention plot had on average slightly over 500, and conventional thinning plots slightly over 250 (Fig. 5). This means that the retention level of understory spruces on understory retention plots was twice as high as intended, and on conventional thinning plots as high as intended under the understory retention treatment. Forest thinning reduced the total BA by ca. 40% with a reduction in all tree type groups and the visibility increased by ca. 60%. The number of understory spruces was reduced by ca. 50%.

4. Discussion

This is the first experimental evaluation of the short-term effects of conventional forest thinning and retention methods on bird communities in the boreal forest. By using new readily interpretable indicators for before-after control-impact experiments, we were able to thoroughly examine whether an observed change in bird occurrence, nest box occupancy and reproductive output in *P. major* was likely causally related to a thinning treatment and whether pre-experimental differences between control and impact plots existed, (Box 1; Chevalier et al., 2019). Using these methods, we provide strong experimental evidence that conventional forest thinning negatively impacts the bird community, with negative effects across guilds and population trend groups with ~ 20% of the species showing clear negative responses. Complete retention plots and understory retention thinning, as applied in this experiment with twice the understory retention level compared to Eggers & Low (2014), have the potential to largely alleviate the negative effects of conventional thinning. They can therefore serve as biodiversity retaining methods during commercial thinning in boreal forests. In this study we aimed, among other aspects, at testing the bird community's response to understory retention thinning as suggested by Eggers & Low (≥250 spruces with live branches below 2 m above ground; Eggers and Low, 2014). However, our forest measurements suggest that this method is already implemented in the conventional thinning routines in the region where the experiment took place, and that in our experiment, twice as many understory spruces were retained in the understory retention treatment compared to what is recommended by Eggers & Low (2014). We urge the reader to bear this difference in mind while we discuss the effects of conventional thinning and understory retention, as applied in our study, on the forest-dwelling bird community of boreal Fennoscandia.

4.1. Guilds and population trend groups

That conventional thinning results in such negative responses across the bird community is novel. We expected that birds living in the canopy would be less affected than ground nesters and foragers because ground-living birds are more dependent on understory cover (Willson and Comet, 1996), which is removed during conventional thinning. Similarly, species related to structurally trivial or deciduous forests were equally affected as species relying on structurally complex forests, even though conventional thinning led to a reduction in structural complexity (reduction in basal area, visibility, and number of understory spruces) which these guilds especially rely on. One explanation for the broad decline in occupancy could be the very large reduction of tree biomass (reduction in total tree basal area) after compared to before thinning. This reduction could lead to a lower ecosystem productivity with less food and nesting opportunities for all bird guilds (Scheiner and Willig, 2005), and not only for those relying on structurally complex forests. However, except for the number of understory spruces, the decrease in tree biomass and increase in visibility was similar on understory retention and conventional thinning plots. However, the bird community did not respond negatively to understory retention. Since conventional thinning and understory retention plots were only different in the number of understory spruces retained, we infer from this that understory density plays an important role for birds in young managed forests. This result gives experimental support for earlier studies that point out a dense vegetation below 3 or 5 m above ground as crucial for bird diversity in boreal forests (Griesser et al., 2007; Klein et al., 2020a, 2020b; Lindberg et al., 2015). This result further suggests the application of understory retention thinning with double the retention level, as applied in our study, but not as suggested by Eggers & Low (2014), as a biodiversity retention measure. The differences between the bird guilds' responses to conventional and understory retention thinning were not strong. This was most likely because the difference in the change in understory spruces due to thinning was not larger between the two treatments and because our understory retention treatment did specifically retain deciduous trees and dead wood, forest structural elements that are known to be crucial to biodiversity (Nilsson et al., 2001). In comparison to conventional thinning, complete retention plots, on which these structural elements are retained, had a more positive effect on birds than understory retention thinning and is most likely the more effective biodiversity retention method.

The reason why neither understory retention thinning nor complete retention positively impacted the bird community can, besides the level of retention not being of sufficient magnitude (Gustafsson et al., 2010), also be related to the fact that we measured only the short term (one year post treatment) responses of birds. The differences between treatments' effects as well as between the reactions of guilds to the treatments could diverge more in the long term as differences in the structural complexity between treatments increase (higher amount of deciduous shrubs on conventional thinning but also understory retention thinning plots due to higher light penetration; Bartemucci et al., 2006; higher tree mortality on complete retention plots and understory retention thinning due to higher competition between remaining trees; Kuuluvainen, 2002). A similar explanation might be valid for the fact that population trend groups did not show differential responses to the treatments. In fact, the abundance trends of forest generalists as well as specialists have increased in Sweden, possibly because of a documented increase in important forest structures at the national scale (Ram et al., 2017).

4.2. Individual bird species

Among species with clearly negative BACI contrasts connected to conventional thinning, only *P. montanus* and *Regulus regulus* have exhibited negative population trends (Ottvall et al., 2009). In contrast to the other birds that reacted negatively, *P. montanus* and *R. regulus* are restricted to forest interior habitats and thinning might therefore be a strong contributor to these bird species' population decline. This is however not true for *Lophophanes cristatus,* which is a strict forest interior species but has not declined in Sweden. Eggers & Low (2014) showed that nest and adult survival in *L. cristatus* were unaffected by a decreasing structural complexity. That we nevertheless saw a strong negative response of this species to conventional thinning might be due to a short-term decrease in occupancy that does not challenge the species long-term viability. Among the species that responded negatively to conventional thinning at the stand level, *P. montanus* was the only one for which complete retention plots did not alleviate the decrease. In fact, *P. montanus* was the only red-listed species that reacted negatively to any of the treatments. However, neutral CI-contribution values (Box 1) indicated uncertain causality, and neutral CI-divergence values indicate that *P. montanus* before the experiment was more common on the, compared to 'no forestry', denser and younger experimental stands. That *P. montanus* is very sensitive to the amount of structurally complex and dense forests in the landscape was the result of a correlative study on its demography and has led to suggestion of understory retention as a thinning method (Eggers and Low, 2014). That absence of a reaction of *P. montanus* to understory retention thinning might be because complete retention plots were not a suitable control due to the strong decline of this species during the experiment even on complete retention plots. Therefore, we do not draw any conclusions on the conservation efficiency of understory retention thinning for *P. montanus*.

4.3. Nest boxes

Except for *C. caeruleus*, we did not observe strong responses in nest box occupancy. We neither observed any differences in the reproductive output of *P. major*. Nesting opportunities for hole-nesting birds are rare in the young managed forests we studied, probably already before thinning. The provisioning of nest boxes might have filled this habitat gap and the positive effect of nesting site availability might have overshadowed any possible effects of the change in vegetation around the nest boxes. Another reason why no major effects were observed might be that while nest site protection decreased due to thinning, insect food availability might have increased due to higher heat fluxes in the more open thinned forests (Jactel et al., 2019), with no directional change in habitat quality as the result.

4.4. The study design

In this study, we used a two-level experimental design where at level one; conventional thinning and complete retention plots were evaluated against ‘no forestry’ plots, and at level two; conventional thinning and understory retention thinning were evaluated against complete retention plots within otherwise conventionally thinned stands. This design allowed us to test two retention measures simultaneously and to evaluate whether the responses of birds to conventional thinning was scale dependent. That the effect of conventional thinning at the stand scale was consistently more negative than at the plot scale, confirms the reasonable assumption that thinning a larger area strengthens the negative effects of thinning. The fact that conventional thinning in the surroundings of complete retention plots affected bird occurrence negatively even on the complete retention plots could mean that complete retention plots were unsuitable controls for the comparison of conventional thinning at the plot level with understory retention. However, since conventional thinning, understory retention and complete retention treatments were equally affected by conventional thinning on the forest stand surrounding the treatment plots, and since the use of complete retention plots as a control represents a classical experimental design (Underwood, 1997), we regard them a good control to evaluate conventional and understory retention thinning at the plot level. Also, in support of complete retention plots being a good control are the largely positive CI-divergence values where negative BACI-contrasts were observed for conventional thinning. A weakness of our design is that the plot size of ∼ 1 ha is smaller than the home range of many species we have analysed here. This is a consequence of the two-level experimental design and is a possible reason why we did not observe stronger effects for the understory retention treatment. However, even if a plot makes up only a share of a birds home range, changes in the forest structure on this plot can affect this species’ occupancy in this part of its home range and the relationship between thinning and occupancy becomes detectable.

4.5. Thinning in other coniferous forests

This is the first experimental study that evaluates the effects of forest thinning on the bird community in boreal forests. The results of this study can therefore only be put into the context of correlative studies, as discussed above (Klein et al., 2020b; Lindberg et al., 2015), or experimental studies from coniferous forests in other regions. In Douglas fir *Pseudotsuga menziesii* stands in western Oregon for example, a largely positive effect of various thinning intensities on bird diversity was found, both in the short and long term (Hayes et al., 2003). They argue that the mechanism behind this increase is an increase in structural complexity due to increased light penetration after thinning. In contrast, we see a decrease in structural complexity due to thinning, at least in the short term. As previously discussed, we only surveyed the birds for one season directly after thinning, which likely does not capture potential differential long term effects among the species in our study. However, Hayes et al. (2003) did not find such a change in the bird community composition during seven years post thinning in the study in Oregon. At a broader scale though, in a *meta*-analysis of the effect of precommercial as well as commercial thinning on biodiversity across North America (excluding boreal), birds reacted negatively only in those studies that looked at short term effects, while all others reported neutral to positive responses (Verschuyl et al., 2011). To conclude with certainty about the effects of conventional thinning and retention methods on the bird community in managed boreal forests of Fennoscandia, we will perform a long-term follow-up evaluation of the bird species’ responses during the coming 20 years.

5. Conclusion

The development of forestry during the last century in Fennoscandia can be used to anticipate the consequences for biodiversity if other regions of the boreal forest choose a similar path. Similarly, the effect of mitigation measures can be most efficiently tested in the drastically simplified managed boreal forests of Fennoscandia, and provide guidelines for which path to take for other boreal regions. With this study we show that conventional thinning leads to a reduced forest structural complexity and has negative consequence across bird guilds, at least in the short term (1–2 years post thinning). Performing understory retention thinning with double the retention level as previously suggested or combining conventional thinning with complete retention plots of ca. 1 ha are measures that can contribute to halting the negative effects of conventional thinning on the occurrence of birds in managed boreal forests in Fennoscandia.

CRediT authorship contribution statement

Julian Klein: Conceptualization, Methodology, Data curation, Formal analysis, Visualization, Investigation, Writing – original draft, Writing – review & editing. **Matthew Low:** Formal analysis, Writing – review & editing, Supervision. **Jörgen Sjögren:** Funding acquisition, Writing – review & editing, Supervision. **Sönke Eggers:** Funding acquisition, Supervision, Conceptualization, Methodology, Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

See the Table A.1, A.2, A.3

Table A.1
To see if a the 20 min break between the two five minutes sampling sessions in 2017 can be reduced to a five minutes break, we analysed whether any species' time of first observation during the whole 30 min observation time in 2017 is consistently beyond 15 min, using a *t*-test. Only species with >2 observations were used.

species	mean	std. error	p_value	sample size
Anthus trivialis	10.11	1.55	0.998	22
Certhia familiaris	11.93	1.06	0.997	69
Chloris chloris	14.96	3.33	0.505	11
Coccothraustes coccothraustes	12.53	2.62	0.805	6
Cyanistes caeruleus	9.579	0.63	1	190
Erithacus rubecula	8.156	0.62	1	236
Ficedula hypoleuca	10.09	2.2	0.981	19
Fringilla coelebs	5.947	0.4	1	337
Lophophanes cristatus	11.28	0.67	1	177
Muscicapa striata	14.6	2.43	0.564	17
Parus major	6.73	0.43	1	308
Periparus ater	12.43	1.03	0.993	82
Phylloscopus sibilatrix	11.75	6.25	0.673	3
Phylloscopus trochilus	8.672	1.35	1	45
Poecile montanus	11.73	1.03	0.999	86
Prunella modularis	10.73	1.08	1	60
Pyrrhula pyrrhula	14.98	2.47	0.503	14
Regulus regulus	10.26	0.62	1	208
Sitta europaea	13.43	1.35	0.875	47
Sylvia atricapilla	12.44	1.84	0.913	28
Troglodytes troglodytes	8.462	0.96	1	78
Turdus merula	11.11	1.01	1	80
Turdus philomelos	11.73	1.34	0.991	49
Turdus viscivorus	11.3	2.25	0.941	18
Anthus trivialis	10.11	1.55	0.998	22
Certhia familiaris	11.93	1.06	0.997	69
Chloris chloris	14.96	3.33	0.505	11
Coccothraustes coccothraustes	12.53	2.62	0.805	6

Table A.2
We show the bird names, their abbreviations used in the analysis, their guilds (Forsman et al., 2010; Ottwall et al., 2009; Wesołowski et al., 2015) and Swedish population trends classification (Lindström, 2017).

latin name	abbrev.	food	foraging	nesting	forest	trend
Anthus trivialis	trapa	insectivore	ground	ground	trivial	negative
Certhia familiaris	trake	insectivore	bark	hole	complex	negative
Chloris chloris	gronk	omnivore	ground/canopy	canopy	trivial	negative
Coccothraustes coccothraustes	stenk	omnivore	canopy	canopy	deciduous	none
Cyanistes caeruleus	blams	insectivore	canopy	hole	deciduous	positive
Erithacus rubecula	rodhe	insectivore	ground	ground	trivial	negative
Ficedula hypoleuca	svare	insectivore	canopy	hole	trivial	negative
Ficedula parva	minde	insectivore	canopy	hole	complex	none
Fringilla coelebs	bofik	omnivore	ground/canopy	ground	trivial	negative
Lophophanes cristatus	tofss	insectivore	canopy	hole	complex	negative
Muscicapa striata	grafe	insectivore	canopy	canopy	trivial	negative
Parus major	talge	insectivore	canopy	hole	deciduous	negative
Periparus ater	svars	insectivore	canopy	hole	trivial	negative
Phoenicurus phoenicurus	rodst	insectivore	canopy	hole	complex	none
Phylloscopus sibilatrix	grone	insectivore	canopy	ground	deciduous	negative
Phylloscopus trochilus	lovse	insectivore	canopy	ground	deciduous	negative
Poecile montanus	talla	insectivore	canopy	hole	complex	negative
Poecile palustris	entia	insectivore	ground/canopy	hole	complex	negative
Prunella modularis	jarnv	insectivore	canopy	canopy	trivial	negative
Pyrrhula pyrrhula	domhe	omnivore	canopy	canopy	trivial	negative
Regulus regulus	kungl	insectivore	canopy	canopy	trivial	negative
Sitta europaea	notva	omnivore	bark	hole	deciduous	positive
Sylvia atricapilla	svara	insectivore	ground/canopy	ground	trivial	positive
Sylvia borin	trase	insectivore	ground/canopy	ground	trivial	none
Sylvia curruca	artse	insectivore	canopy	canopy	deciduous	negative
Troglodytes troglodytes	gardg	insectivore	ground	ground	trivial	positive
Turdus iliacus	rodvt	insectivore	ground	canopy	trivial	negative
Turdus merula	koltt	insectivore	ground	canopy	trivial	positive
Turdus philomelos	taltt	insectivore	ground	canopy	trivial	none
Turdus viscivorus	dubbt	insectivore	ground	canopy	trivial	positive

Table A.3
We compared the probability of occurrence on impact (Conventional, Complete retention, Understory retention) plots with control (No forestry) plots before thinning for all bird species. The median and the 95% CIs are shown. A positive value indicates that the probability of occurrence on control plots was higher than on impact plots.

latin name	median	2.5%	97.5%
Anthus trivialis	0.05	−0.35	0.41
Certhia familiaris	0.05	−0.27	0.33
Chloris chloris	0.03	−0.41	0.38
Coccothraustes coccothraustes	0.03	−0.39	0.37
Cyanistes caeruleus	0	−0.25	0.14
Erithacus rubecula	−0.02	−0.2	0.06
Ficedula hypoleuca	0.02	−0.45	0.43
Ficedula parva	0.01	−0.61	0.32
Fringilla coelebs	0.01	−0.14	0.12
Lophophanes cristatus	0.01	−0.11	0.1
Muscicapa striata	0.05	−0.44	0.47
Parus major	0.02	−0.12	0.16
Periparus ater	0.02	−0.3	0.22
Phoenicurus phoenicurus	0.04	−0.37	0.4
Phylloscopus sibilatrix	0.04	−0.35	0.38
Phylloscopus trochilus	−0.26	−0.68	0.09
Poecile montanus	−0.18	−0.65	0.03
Poecile palustris	0.02	−0.66	0.38
Prunella modularis	0	−0.33	0.19
Pyrrhula pyrrhula	0.03	−0.36	0.33
Regulus regulus	−0.01	−0.19	0.09
Sitta europaea	−0.01	−0.3	0.16
Sylvia atricapilla	0	−0.52	0.27
Sylvia borin	0.03	−0.46	0.36
Sylvia curruca	0.02	−0.58	0.35
Troglodytes troglodytes	0.22	−0.11	0.52
Turdus iliacus	0.03	−0.39	0.39
Turdus merula	0	−0.27	0.18
Turdus philomelos	0.03	−0.28	0.28
Turdus viscivorus	0.02	−0.56	0.36

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