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Broadleaf retention benefits to bird diversity in mid-rotation conifer production stands

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ABSTRACT

Retention forestry involves saving important forest structures for flora and fauna during the final felling of a stand, including dead wood and variable amounts of living trees, i.e. green tree retention (GTR). Here we evaluate the long-term effects on avian diversity from GTR by surveying forest birds in 32 mid-rotation stands in southern Sweden, in which broadleaf GTR was present or absent. Complementing the many studies that have assessed GTR in clear-cuts, our results indicated that bird assemblages can also benefit from broadleaf GTR several decades after final felling in conifer dominated production stands. The GTR stands harboured a higher bird abundance and species richness than the control stands without GTR, and also appears to have benefited several important guilds, such as broadleaf-associated birds and cavity nesters. However, variation in the number trees retained, the species composition of retained trees, and their environmental context within the stand (e.g. density and proximity of surrounding production trees), limited our capacity to detect threshold requirements for GTR. In summary, our study provides a "glimpse into the future" as mid-rotation production stands with such old and large retained trees are unusual in today's landscape, but are expected to become more common in the decades to come, in Sweden and many other nations. Our study thereby provides provisional support for the continued and future use of this practice, and indicates that the biodiversity contribution of retention trees continues to occur several decades into the stand's rotation.

1. Introduction

Forests cover 30% of the world's land area, are fundamental source of habitat for biodiversity, and provide a large variety of ecosystem service benefits to humanity. With only 18% of the world's forests formally protected (FAO, 2020), the majority of forest land is used for the provision of a variety of goods and services. One such important service is timber production, an activity that often comes in conflict with biodiversity (Lindenmayer and Franklin, 2002). Consequently, a large number of forest species are declining and many are threatened by extinction (Ceballos et al., 2017; IPBES, 2019). As a conservation measure intended to reduce the negative impact of intensive forestry, the concept of "retention forestry" emerged in North America in the 1980s (Franklin, 1989), and the practice is now widely applied in production forests in many parts of the world (Gustafsson et al., 2012; Lindenmayer et al., 2012; Fedrowitz et al., 2014). Retention forestry involves saving important forest structures for flora and fauna during the final felling of a stand. These structures include dead wood in the form of logs, snags, and stumps, and importantly, variable amounts of living trees, i.e. green tree retention (hereafter GTR).

The ecological rationale underlying GTR is that living trees should i) act as "life-boats" during the early phases of the stand rotation for organisms dependent on the continued availability of mature trees, ii) maintain old-growth structural features, e.g. coarse bark, trunk cavities and coarse branches, throughout the stand's rotation period, and iii) function as "stepping-stones" to enhance dispersal and connectivity in managed landscapes (Harris, 1984; Franklin et al., 1997). A large number of studies have evaluated the capacity of this practice to mitigate forestry impacts on biodiversity (Rosenvald and Lõhmus, 2008; Gustafsson et al., 2010; Fedrowitz et al., 2014), across a variety of species groups including insects (Horák, 2017; Koch Widerberg et al., 2018), lichens (Hofmeister et al., 2016), and birds (Gutzat and Dormann, 2018; Basile et al., 2019; Kebrle et al., 2021). However, since the practice is relatively new, most of these studies focus on conservation benefits soon after final felling (Söderström, 2009). Hence, even though the success of the method needs be evaluated over longer time periods –

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due to both the length of forestry rotation times and retention tree lifespans - the long-term utility of retention practices for biodiversity remains largely unknown.

Lack of knowledge regarding the longer term implications of GTR is particularly acute for forest bird communities. This is despite the fact that birds are important for biodiversity and useful for conservation studies as they; i) fulfil many important ecological functions, e.g. seed dispersal, pest control, and pollination, ii) respond quickly to changes in their environment, iii) are relative easy to survey, and iv) are charismatic, which readily attracts public interest and research support (Sekercioglu et al., 2016). In Sweden, a study conducted in the 1–8 year window after final felling, found a higher abundance of resident birds on clear-cuts with many retained trees, compared to those with few or no retained trees (Söderström, 2009). With respect to the species of tree retained, some cavity-nesting species, e.g. great spotted woodpecker (*Dendrocopos major*), spotted and pied flycatcher (*Muscicapa striata* and *Ficedula hypoleuca)*, blue tit (*Cyanistes caeruleus*), and nuthatch (*Sitta europaea*) were more common on clear-cuts with many retained broadleaf trees, while other birds (e.g. willow (*Poecile montanus*) and crested tit (*Lophophanes cristatus*)) preferred clear-cuts with retained conifers. Notably, some ground-nesting migratory birds appeared to prefer clear-cuts with fewer retained trees (e.g. wood lark (*Lullula arborea*) and whinchat (*Saxicola rubetra*)) (Söderström, 2009). Studies conducted in Canada (Schieck and Hobson, 2000) and Estonia (Rosenvald and Lohmus, 2007) have obtained similar results for stands recently felled. In a compilation of research from around the world on GTR and birds, 80% of studies were carried out less than 20 years after final felling (Rosenvald and Lõhmus, 2008), with a more recent review confirming the general lack of studies of GTR implications for bird communities later in the rotation (Basile et al., 2019).

Sweden is a country well suited to research on how GTR affects biodiversity. Seventy percent of the country is covered by forest; most of which is used for industrial forestry, and primarily managed using intensive even-aged monocultures of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) over rotation periods of 45–120 years (Felton et al., 2020). As a result, almost all forests are industrially managed for wood production, and the 6% of productive land that are protected are embedded mainly in landscapes dominated by production stands (Svensson et al., 2018). GTR started in Sweden on a larger scale in the mid-1990 s when a new legislation was implemented, and new non-governmental environmental certification schemes (FSC, PEFC) were embraced by many forest owners (Sténs et al., 2019).

Sufficient time has now elapsed to assess how GTR affects biodiversity half-way through a silvicultural rotation, and at a point in time when the benefits to birds from retention trees may be diminished by their placement within middle-aged production stands. Here we used these circumstances to evaluate the long-term effects on avian diversity from GTR by surveying forest-nesting birds in 32 stands in southern Sweden, which were final felled and planted with Norway spruce in the early and mid 1990s (i.e., now 25–30 years old and approximately half way through the rotation period). Half of the stands (16) had broadleaf GTR at the time of final felling, whereas control stands lacked GTR. We focused on retained broadleaves because they have a higher potential to benefit bird diversity than do retained conifers, largely due to the historic loss of broadleaf dominated forests in this region (Lindbladh et al., 2014a), and the prevalence of bird species that are broadleaf associated (Roberge and Angelstam, 2006; Felton et al., 2010), and reliant on habitat and resources not provided by conifer production trees (Felton et al., 2021). Specifically, large older broadleaf trees may provide important tree-related microhabitats, such as particular bark conditions, cracks and cavities (Basile et al., 2020; Asbeck et al., 2021) that cannot be found in conifer production stands lacking GTR.

We hypothesize that:

I. Stands with large broadleaf GTR will have significantly higher bird diversity than stands without GTR. This expectation is based on previous studies showing that even relatively small number of broadleaved trees in the coniferous production forest positively affects bird diversity (Lindbladh et al., 2017; Felton et al., 2021).
II. Bird species associated with broadleaf trees will benefit more than conifer-associated birds.
III. Woodpeckers will also benefit from broadleaf GTR, due to their association with old trees and dead wood (Roberge et al., 2008).
IV. Large variation in the amount of retention trees, their species composition and micro-habitats will lead to more diverse bird communities (beta-diversity) among the GTR stands than among the control stands.

Overall, we expect that conservation efforts involving with GTR will have a positive impact, but that the strength of these benefits will vary with the amount, type, and size of tree species retained at final felling.

2. Material and methods

2.1. Study area

The study was conducted in the hemi-boreal zone of southern Sweden (Ahti et al., 1968). The mean temperature (1961–1990) in the area is approximately −1 °C in January, and 17 °C in July, with precipitation at 700–1200 mm/year. Forests cover 63% of the land area in the region (Nilsson et al., 2020). The landscapes of southern Sweden have undergone dramatic changes during the last 50–400 years. From domination by traditional cultural landscapes with open and grazed forests of mixed tree species, the region is today largely covered by dense conifer-dominated managed forest stands (Lindbladh et al., 2011). This borealization process is the result of a combination of anthropogenic (the agricultural revolution, forest grazing by livestock, silviculture, etc.) and natural (climate, species immigration, etc.) drivers (Lindbladh et al., 2014a). About 2% of the productive forest land (timber production capacity >1 m^3 ha^{-1} $year^{-1}$) in southern Sweden is formally protected (Nilsson et al., 2020). Norway spruce dominates the standing volume (46%), closely followed by Scots pine (30%). Conifer dominated production forests are generally planted with improved plant material in even-aged stands after soil scarification, and pre-commercially and commercially thinned two to three times during a rotation (Felton et al., 2020). The main purpose of pre-commercial thinning is to remove any undesired excess of naturally regenerated broadleaves, mainly birch (*Betula* spp.). Norway spruce stands are clear-cut after a rotation period of 45–70 years, depending in-part on site conditions (Felton et al., 2017). Birch is the third most common tree (11%) in the region (Nilsson et al., 2020). Less common trees are oaks (*Quercus* spp.; 4%), aspen (*Populus tremula*; 2%), alder (*Alnus glutinosa*; 3%) and beech (*Fagus sylvatica*; 2%).

The majority of production forests in Sweden are certified by voluntary certification schemes (i.e. FSC or PEFC, 45% and 56% of forest area respectively) (Lehtonen et al., 2021). The Swedish standards of FSC and PEFC, and the forest legislation, require that trees valuable for conservation of biodiversity are left during final felling. According to certification standards, at least 10 living trees per hectare must be retained at this time (PEFC, 2016; FSC, 2020).

2.2. Stand selection and categorizations

Identifying production stands based on the extent and type of GTR conducted is difficult, because these features are not registered by any authority, and no databases are available. The stand data available from forest owners are typically limited to information directly related to silvicultural prescriptions, and not provided at the level of individual trees. For this reason, large retained trees are usually not registered. In order to find suitable stands we used an orthophoto-based (aerial photos geometrically corrected) methodology developed by us (Holmström et al., 2020). Photos from 1990 to 1996 were used to identify stands that underwent final felling at the time Sweden's legal requirements for broadleaf GTR were changed, and the certification schemes were implemented. Stands were identified and categorized by which broadleaved trees were retained (GTR stands), as well as requiring nearby stands that lacked broadleaf GTR (control stands) (Fig. 1). We chose a paired design to facilitate the bird surveys (see below). Modern orthophotos of the same stands were then used to check if the retained broadleaves were still present in treatments, with additional confirmation provided by subsequent field visits. In total 16 pairs of stands were selected, with GTR and control stands located between 1.3 and 13.5 km from each other. Stand size varied from 3.0 to 10.3 ha (mean 6.0 ha), with no difference in mean size between GTR stands and controls (5.4 *vs* 9.3 ha, p-value = 0.07). The minimum size of 3 ha was set to reduce the prevalence of birds associated with a stand's border zone vegetation.

2.3. Bird surveys

All surveys were done using the point count survey method (Bibby et al., 2000). We used a survey radius of 30 m as this threshold distance limits the birds included to only those located within the stand, and reduces the risk of double counting birds at two survey points. Furthermore, this radius is less than the maximum distance observers are estimated to be able to properly assess the distance to calling birds (i.e. 65 m, see Alldredge et al., 2007). Four survey points were located within each stand, with the proviso that the distance between two survey points was 60 m, and at least 50 m from the stand edge. The points were clustered towards the centre of the stand, which reduced the influence of bird assemblages found in stand edges. This placement also avoids survey points being placed over larger areas in larger stands, and thereby inflate avian diversity results due to the range of environments

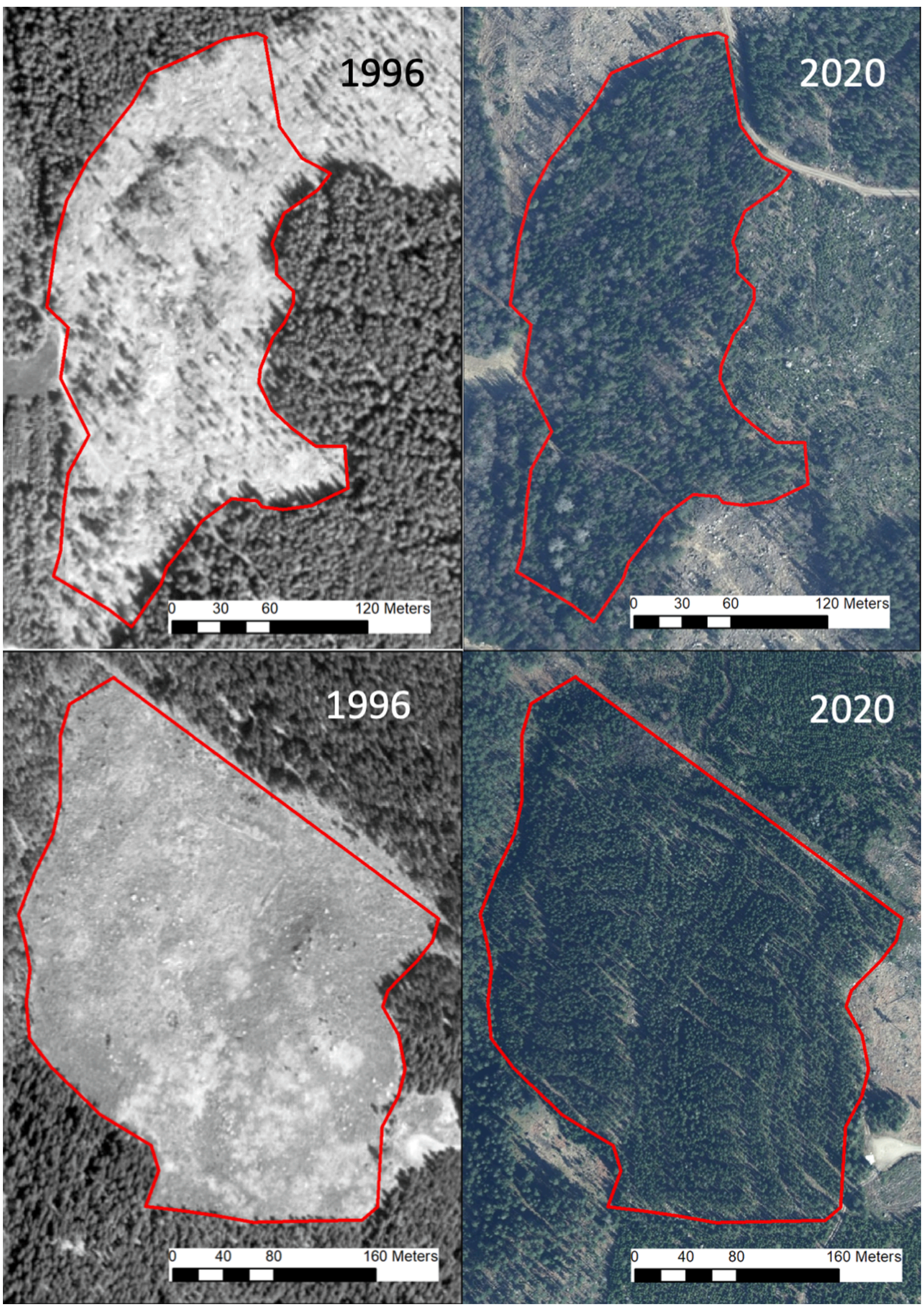

Fig. 1. Example stands to illustrate the suitable stand identification process used in the study. The stand (371) in the top row harboured retained trees after final felling in the 1990s, seen mostly to the left in the orthophoto from 1996. These large broadleaves can also be seen in the photo from 2020, but were by this time intermixed with planted spruce trees. The control stand (686 K) in the bottom row had large trees neither in the 1996 orthophoto, nor in the 2020 photo, and thereby predominantly includes planted spruce trees.

surveyed. We surveyed each stand four times to cover the activity of early and late season breeders; twice in early spring (late March) and twice in late spring (mid-May).

All point count surveys were conducted by ornithologists (ML, JE, AF) experienced with both bird identification and point count surveys, which is important to ensure data quality (Farmer et al., 2012). Most identification was made acoustically rather than visually. In cases of uncertainty with respect to the number of individuals calling, the most conservative estimate of abundance was used. All birds encountered were noted, but only individuals performing territorial behaviour (song in almost all cases) were included in data analyses. This was done in order to increase our confidence that an individual's occurrence was tied to the vegetation conditions within the stand. The survey results from the four points in each stand were combined, hence the stand is treated as one observation. As an estimate of the abundance of each bird species in a given stand (based on the four survey points combined in each stand), we used the highest value obtained for each species from the four separate surveys conducted in each stand. We adopted this approach because research indicates that true avian abundance is best correlated with maximum rather than average abundance data from repeated surveys (Toms et al., 2006).

Additional survey protocols were made to capture the occurrence of woodpeckers, due to their specialisation and high requirements for structures that are often uncommon in managed forests (Roberge et al., 2008). We therefore noted woodpeckers not only within the plots, but all individuals encountered in the stands, showing territorial behaviour or not, during the combined survey period.

2.4. Bird ecological characteristics

We used descriptions in Birds of the World (https://birdsoftheworld.org/bow/home) adjusted to reflect regional species-specific autecological affinities (Ottosson et al., 2012) to classify birds in guilds as based on migratory status, forest habitat associations, and nest site preference (Table 1). Bird species were classified as migrants (only present in the study area during the breeding season), partial migrants (some individuals in the regional population being migratory, others resident), or residents (present in the study region throughout the year). Bird species were also classified according to their affinity regarding forest (habitat) type, i.e. broadleaf specialist, generalist or coniferous specialist. They were further classified according to nest placement, i.e. ground nesters, above ground nesters, and cavity nesters. We classified species by conservation status using the Swedish Red List (Artdatabanken, 2020).

2.5. Broadleaf GTR

The diameter at breast height (DBH) of all retained broadleaf trees ≥20 cm DBH was measured throughout the stand. In order to avoid mistaking fast-growing birches and aspens established after final felling, with broadleaf GTR, their threshold size DBH was raised to ≥25 cm. The average number of retained broadleaf stems in treatment stands was 17.4 per hectare, but with large variation between stands (Fig. 2). The most common retained tree species were birch, beech and oaks. Two control stands had a small number of large broadleaf trees, but it was not known whether these were retained at the time of final felling in the

Table 1
Number of GTR and control stands each bird species was encountered in during the surveys. GTR and controls are stands with and without retained broadleaves, respectively. Number of individuals in parenthesis. NT is 'nearly threatened' according to the Swedish 2020 red-list. Migratory habits: M = migrant, PM = partial migrant, R = resident (classification based on regional data). Forest habitat preference: B = broadleaf associated, C = conifer associated, B/C = generalists breeding in mixed conifer/broadleaf forests). Nest placement: AG = above ground, GN = ground nesting, CN = cavity nesting.

Species (red-list status)	*Scientific name*	Migratory habit	Forest habitat preference	Nest site preference	No of GTR stands with occurrence (individuals)	No of control stands with occurrence (individuals)
Western Capercaillie	*Tetrao urogallus*	R	C	GN	0 (0)	1 (1)
Black Grouse	*Tetrao tetrix*	R	B/C	GN	1 (2)	0 (0)
Common Wood Pigeon	*Columba palumbus*	M	B/C	AG	9 (9)	3 (3)
Tawny owl	*Strix aluco*	R	B	CN	1 (1)	0 (0)
Great Spotted Woodpecker	*Dendrocopos major*	R	B/C	CN	1 (1)	1 (1)
Lesser spotted woodpecker (NT)	*Dendrocopos minor*	R	B	CN	–	–
Black Woodpecker (NT)	*Dryocopus martius*	R	B/C	CN	2 (2)	0 (0)
Eurasian Jay	*Garrulus glandarius*	R	B/C	AG	8 (10)	5 (5)
Willow Tit (NT)	*Poecile montanus*	R	C	CN	6 (8)	5 (5)
Coal Tit	*Periparus ater*	R	S	CN	12 (14)	7 (7)
European Crested Tit	*Lophophanes cristatus*	R	C	CN	4 (4)	9 (9)
Marsh Tit (NT)	*Poecile palustris*	R	B	CN	1 (2)	0 (0)
Eurasian Blue Tit	*Cyanistes caeruleus*	R	B	CN	4 (4)	1(1)
Great Tit	*Parus major*	R	B/C	CN	11 (13)	5 (6)
Common Chiffchaff	*Phylloscopus collybita*	M	B	GN	1 (1)	1 (1)
Willow Warbler	*Phylloscopus trochilus*	M	B/C	GN	9 (14)	7 (8)
Eurasian Blackcap	*Sylvia atricapilla*	M	B	AG	6 (6)	0 (0)
Goldcrest	*Regulus regulus*	PM	C	AG	12 (18)	11 (19)
Song Thrush	*Turdus philomelos*	M	B/C	AG	5 (5)	5 (6)
Mistle Thrush	*Turdus viscivorus*	M	C	AG	1 (2)	5 (5)
Common Blackbird	*Turdus merula*	R	B/C	AG	5 (5)	4 (4)
European Robin	*Erithacus rubecula*	M	B/C	GN	12 (14)	4 (15)
European Pied Flycatcher (NT)	*Ficedula hypoleuca*	M	B	CN	1 (1)	0 (0)
Eurasian Wren	*Troglodytes troglodytes*	R	B/C	GN	1 (1)	0 (0)
Eurasian Nuthatch	*Sitta europaea*	R	B	CN	2 (2)	0 (0)
Eurasian Treecreeper	*Certhia familiaris*	R	B/C	AG	1 (1)	1 (1)
Tree Pipit	*Anthus trivialis*	M	B/C	GN	1 (1)	1 (1)
Eurasian Bullfinch	*Pyrrhula pyrrhula*	PM	B/C	AG	1 (1)	1 (1)
Common Chaffinch	*Fringilla coelebs*	PM	B/C	AG	13 (19)	10 (18)
Eurasian Siskin	*Carduelis spinus*	PM	B/C	AG	0 (0)	1 (1)

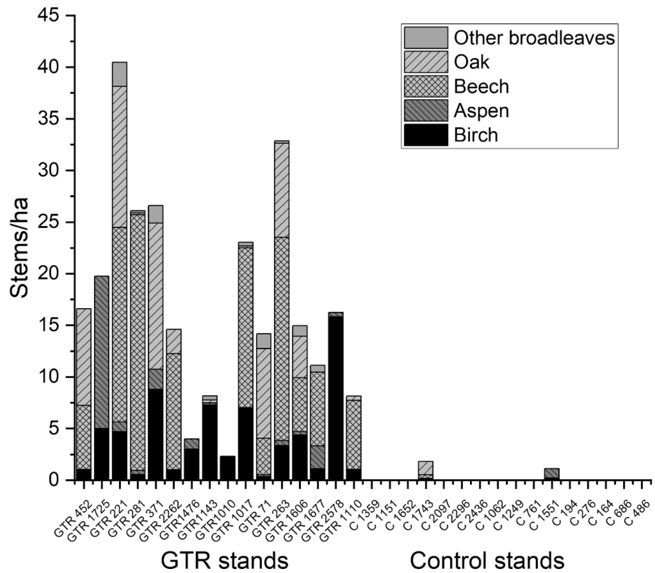

Fig. 2. Number of stems per hectare of different retained broadleaved species in the stands included in the study. GTR and controls are stands with and without retained broadleaves, respectively.

early 1990s.

2.6. Stand survey data

Five to six plots in each stand were surveyed for structural variables provided by production stems (Table 2). The DBH was measured, and basal area calculated, for all living trees ≥1.3 m tall and ≥5 cm DBH, within a radius of 10 m from the centre of the plot; in a few cases 5.64 m radius if the stand was unusually dense. Broadleaf trees larger than ≥20 or 25 cm DBH (see above) were not used in the analysis of the stand, but were included in the analyses as retention trees. All shrubs <5 cm DBH were counted (or estimated if present in very large numbers) within a 10 m radius from the plot centre. The volume of all coarse woody debris (CWD) was quantified by measuring the length and diameter of dead wood items with diameters of ≥10 cm within 10 m (standing dead trees and snags), or 5.64 m (logs; only the section found inside the circle was included), of the plot centre.

2.7. Remote sensing data

The landscape around the stands, including some stand variables, was described using two publicly available remote data sets, SLU Forest map 2015 (SLU, 2015) and NMD 2018 (Naturvårdsverket, 2018). These are based on remote sensing information combined with ground data. The Forest map provides standard forest data, except age, for forest land in 12.5 × 12.5 m pixels, while NMD assigns all land to broad land-cover classes in 10 × 10 m pixels. Using these data sets it was possible, in circles with varying radius, to describe the stand and surrounding land in terms of forest state and land-cover. Since forest age was missing in the data sets, a proxy based on tree height and diameter was used. Both stand survey and remote sensing data were used as environmental variables in the data analyzes (Table 2).

2.8. Data analyzes

All statistical analyzes were done in R, vers. 4.1.2 (R_Core_Team, 2021). We used Generalized Linear Mixed Models (GLMMs), as implemented in the glmmTMB function in the glmmTMB package, to model the effect of stand type (GTR stand *vs*. control) on species richness and total number of individuals, as well as the number of individuals within guilds. For the guild analysis, a separate GLMM was run for each category including, for example, migratory habits and the interaction between migratory habit and stand type. This provided an individual intercept and slope for each guild category. The number of individuals within guilds was used as dependent variable as it down-weighs the effects of single species occurrences in relation to species richness (Felton et al., 2021). In this study, however, the number of individuals was closely correlated with species richness (r = 0.94). Poisson error distribution and log link-function were applied for all response

Table 2
Results for stand variables measured during the on the ground surveys (stand survey data) and using remote sensing data. GTR and controls are stands with and without retained broadleaves, respectively. DBH is diameter at breast height and std DBH is standard deviation of the DBH. CWD is coarse woody debris. P-value refers to T-test results of the difference between the stand types. Stand height variation is the standard deviation of the mean heights among remote sensing survey points inside a stand.

		GTR stands		Controls		
		Mean	Standard error of mean	Mean	Standard error of mean	P-value
	Stand area (ha)	5.4	1.7	4.2	9.3	0.07
Stand survey data	Pine (m^2 ha^{-1})	1.05	1.7	0.45	1.3	0.27
	Spruce (m^2 ha^{-1})	16.50	4.2	14.96	4.1	0.32
	Birch (m^2 ha^{-1})	1.63	1.1	1.28	1.0	0.36
	Aspen (m^2 ha^{-1})	0.000	0.0	0.006	0.0	0.33
	Beech (m^2 ha^{-1})	0.11	0.1	0.00	0.0	0.01 *
	Oak (m^2 ha^{-1})	0.04	0.1	0.006	0.0	0.12
	Other broadleaves (m^2 ha^{-1})	0.04	0.1	0.013	0.0	0.17
	Total (m^2 ha^{-1})	19.4	4.2	16.7	4.2	0.09
	Total % broadleaves	9.3%		8.2%		0.58
	Stand mean DBH (cm)	13.0	1.3	12.8	0.9	0.86
	Std DBH	51	13	38	9	0.002 *
	CWD (m^3 ha^{-1})	4.3	5.4	0.9	1.8	0.03 *
	Shrubs (no ha^{-1})	627	662	392	596	0.31
Remote sensing data	Stand height variation	21.5	3.9	17.6	5.2	0.03 *
	% forest r = 500 m	77.4%	11.2	72.9%	10.2	0.27
	% agriculture (r = 500 m)	0.5%	1.0	1.1%	2.3	0.34
	% old forest r = 500 m	0.4%	1.3	0.9%	2.0	0.26
	% old forest r = 1000 m	0.7%	1.5	0.8%	1.8	1.0
	% volume broadleaves (stand)	28%	0.18	11%	0.06	0.003 *
	% volume broadleaves (r = 500))	19%	0.09	13%	0.06	0.07
	% volume broadleaves (r = 1000))	18%	0.07	13%	0.05	0.045 *

variables. A random effect (intercept) of stand pair (see above) was included in the GLMMs for species richness and abundance, to account for the relative geographical closeness of the pairs, as well as to account for any potential bias in the pairs due to their having the same surveyor, and being surveyed on the same day under the same weather conditions. Preliminary analyzes revealed spatial autocorrelation in the residuals of these models, which is why an exponential correlation structure based on the stand coordinates additionally was introduced. All models were evaluated by plotting the residuals against the predicted values, and by applying tests for overdispersion and spatial autocorrelation. The latter was done through Morańs I test in the ape package (Paradis and Schliep, 2019). Stand survey as well as remote sensing data of the two stand types (Table 2) were compared using t-tests. Variables that differed significantly ($P < 0.05$) between the two stand types were subsequently introduced to the GLMM model structure as described above. In addition to running the model with only "stand type" as an explanatory variable, we also fitted two models with the environmental variables (with and without stand type). Pseudo R-squares according to (Nakagawa and Schielzeth, 2013) were then calculated using the "r.squaredGLMM" function in the MuMIn package (Barton, 2020), and the variance partitioned between the different sets of variables.

A Non-metric Multidimensional Scaling (NMS) was performed on the bird community data (abundances). Three dimensions were required to reduce the stress level (Stress = 0.15). To test for differences in composition between the two stand types we did a permutational Multivariate Analysis of Variance (perMANOVA). The NMS and the perMANOVA were conducted using the metaMDS and Adonis functions respectively. Both were conducted within the vegan package (Oksanen et al., 2020), and with Bray-Curtis distance and 999 permutations. The total beta diversity (Bray-Curtis dissimilarity), balanced variation fraction and abundance-gradient fraction among the stands within stand type were calculated using the beta.sample.abund function in the betapart package (Baselga et al., 2021). The probability of differences between the stand types in terms of total beta diversity and the two fractions, was calculated using 1000 random re-samplings; each excluding three of the 16 observations in each stand type.

3. Results

A total of 272 bird individuals of 29 species exhibited territorial behaviour in the stands within the point count surveys. Species richness and abundance were significantly higher in the GTR stands than in the control stands (Fig. 3ab). No correlation (Pearson r) was found between bird species richness or abundance and the number (richness, $r = -0.45$, $p = 0.078$; abundance, $r = -0.43$, $p = 0.098$) or basal area ($r = -0.37$, $p = 0.155$; $r = -0.37$, $p = 0.153$) of retained broadleaf trees in the GTR stands.

The four most common birds in the GTR stands were chaffinch (*Fringilla coelebs*), goldcrest (*Regulus regulus*), coal tit (*Periparus ater*) and robin (*Erithacus rubecula*), and they were encountered in 12 or 13 of the 16 GTR stands (Table 1). The three most common birds in the control stands were goldcrest (11 of 16 stands), chaffinch (10 stands) and crested tit (7 stands). Four of the bird species encountered are classified as "Near Threatened" (NT) in the Swedish red-list (Artdatabanken, 2020). These are black woodpecker (*Dryocopus martius*), willow tit, marsh tit (*Poecile palustris)* and European pied flycatcher. All NT bird species except willow tit were encountered in GTR stands only. Among the woodpeckers encountered within entire stands (see methods), great spotted woodpecker was found in eight stands (five GTR stands and three controls), black woodpecker in two GTR stands and lesser spotted woodpecker (*Dendrocopos minor*) in one GTR stand (Fig. 4). Both black woodpecker and lesser-spotted woodpecker are on the Swedish red-list.

Regarding the guilds, the broadleaf specialists and species without a preference for either forest habitat type (see Table 1), all had significantly higher abundance in the GTR stands than in the controls (Fig. 5a), but no corresponding difference was found for the conifer specialists.

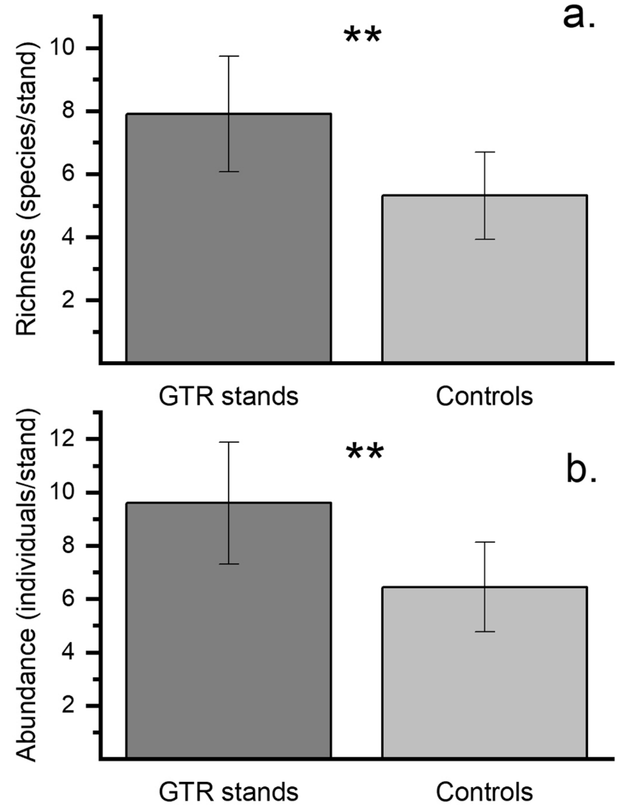

Fig. 3. a. Predicted number of bird species (richness) and b. individuals (abundance) in the 16 GTR and 16 control stands based on generalized linear mixed models. Error bars show ± two standard errors. ** = $P < 0.001$. GTR and controls are stands with and without retained broadleaves, respectively.

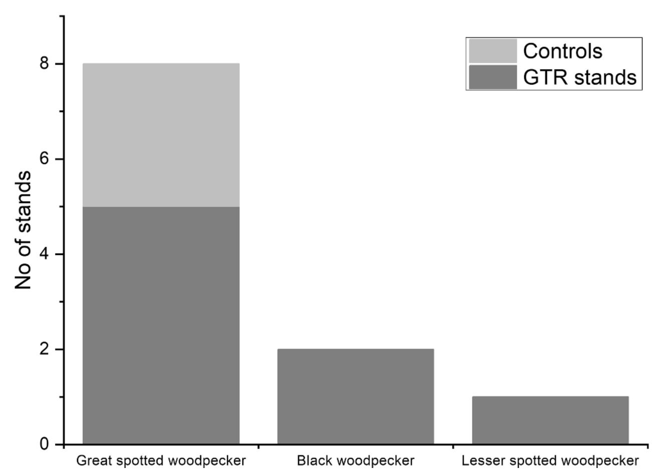

Fig. 4. Number of GTR and control stands where woodpeckers were noted in any part of the stand, i.e. not only within the survey plots. GTR and controls are stands with and without retained broadleaves, respectively.

The most common broadleaf specialists were blue tit, Eurasian blackcap (*Sylvia atricapilla*) and nuthatch. Cavity nesters and ground nesters were also more common in GTR stands as compared to controls (Fig. 5b), whereas no difference was found for the above-ground nesters. Finally, migrants and resident birds were more common in the GTR stands, whereas partial migrants showed no such difference between stand types (Fig. 5c).

With the exception of the retained trees, forest composition and structure were largely similar in the GTR and control stands according to

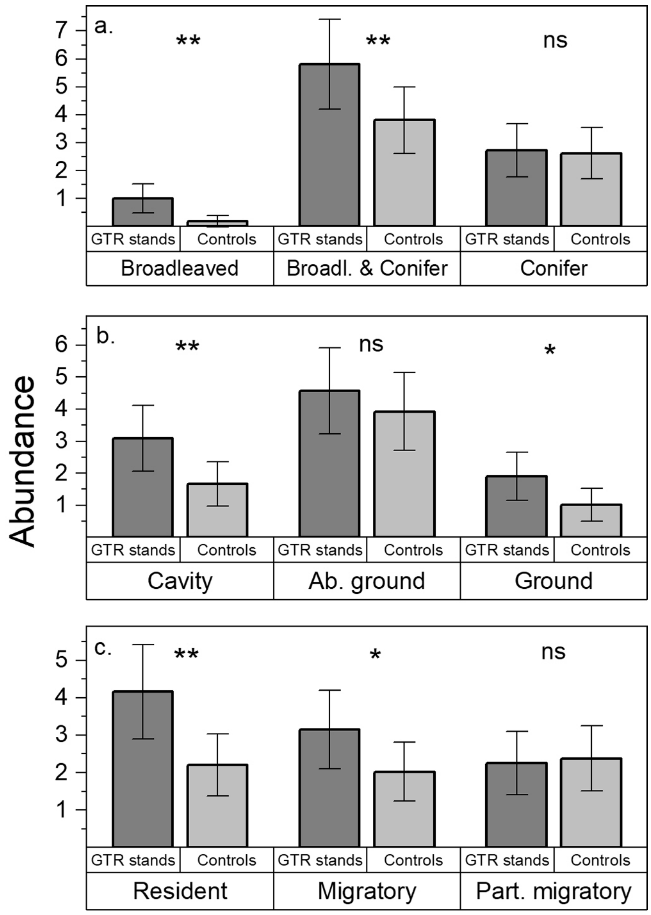

Fig. 5. Predicted number of individuals (abundance) from different bird guilds based on generalized linear mixed models with respect to: a) forest habitat preferences, b) nest site selection, c) migratory habits. Error bars show ± two standard errors. NS = P > 0.05, * = P < 0.01, ** = P < 0.001. GTR and controls are stands with and without retained broadleaves, respectively.

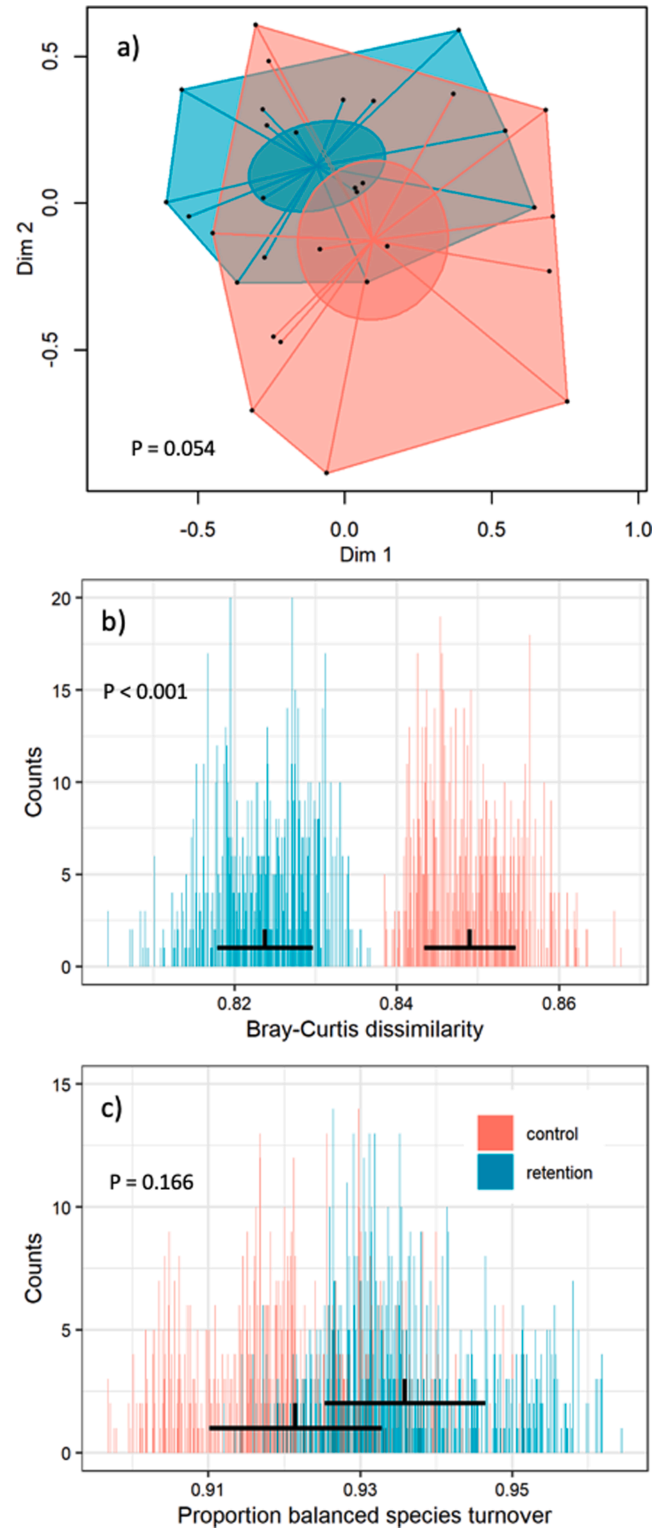

Fig. 6. a) Non-metric multidimensional scaling of the bird assemblages (based on abundances). Points show the position of the stands in ordination space while the polygons show the distribution limits of the two stand types (controls *vs* GTR (with retention trees) stands). Ellipses are 95% confidence intervals around the centroids of the two stand types and P-values indicate the probability of different locations of the centroid. b) Histogram of Bray-Curtis dissimilarities (BCD) from 1000 random re-samplings (n = N-3) performed within each stand type. Black lines show the mean (±SD) BCD of the stand types. c) Like panel b but showing the proportions of the BCDs in panel a that are related to a balanced turnover in species composition.

the stand survey (Table 2). All stands were strongly dominated by spruce. Pine and birch also occurred, but in low numbers, on average never >2 m^2 ha^{-1}. No other tree species exceeded 0.5 m^2 ha^{-1} in any stand. The only significant difference in terms of species composition between GTR stands and controls was the small amount of beech (mean = 0.11 m^3 ha^{-1}) found in GTR stands (absent in the controls). In addition, a wider variation in DBH was observed in the GTR stands, and the volume of dead wood (CWD) was also higher than in controls (Table 2). The remote sensing data identified a significant greater stand height variation in GTR stands than in the controls (both production trees and GTR -trees measured). In terms of landscape context, at a radius of 1000 m, in the surroundings of GTR stands the remote sensing data indicated a significantly higher percentage of broadleaves than in the landscapes surrounding controls.

Stand type alone (GTR *vs* control) explained more of the variation in abundance of birds than the environmental data assessed (both stand survey and remote sensing data). The GLMM of the sole effect of stand type on the number of individuals had an R^2 = 0.21. In contrast, the model including the basal area of beech, DBH variation, CWD, stand height variation had an R^2 of 0.13, whereas including these four variables with the stand type yielded an R^2 of 0.27.

The NMS and multivariate analysis of variance did not show a statistically significant difference (P = 0.054) in bird species composition between the two stand types (Fig. 6a). The NMS did, however, indicate a higher beta diversity among the control stands than among the GTR stands, which was confirmed by the analysis of Bray-Curtis dissimilarity

(BCD, Fig. 6b). The majority of the BCD (92% and 94% for the controls and GTR stands, respectively) among both stand types was constituted by a balanced turnover of species, of which just a minor part (8% and 6%) was due to differences in abundances (Fig. 6c).

4. Discussion

4.1. Bird diversity in GTR stands vs. controls

Our results indicate that bird assemblages benefit from the retention of large broadleaved trees several decades after final felling in conifer production stands. The GTR stands harboured a higher bird abundance and species richness than the control stands (Fig. 3 ab), and the GTR stands also benefited several important guilds, such as broadleaved associated birds (Fig. 5a). Apart from the retained trees, there was no significant difference in the total share of broadleaves between the stand types (except a minor beech component in some GTR stands). For this reason, we suggest that the observed benefits to bird diversity are being driven by the retention of large broadleaves. Conifer forests are a dominating feature of Swedish forestry, and previous studies have shown that relatively small shares, even 15%, of broadleaves added to such production stands can benefit broadleaved associated birds (Lindbladh et al., 2017; Felton et al., 2021). Here we show that although the retained broadleaves on average make up less than 10% of the basal area of the GTR stands, these large trees appeared to have a positive effect on broadleaved associated guilds. Importantly, there was no corresponding decline in conifer specialists. A similar positive influence on bird communities by a higher proportion of larger (DBH $\geq$ 70 cm) retained broadleaves was found in a recent study from the Czech Republic in managed spruce forests (Kebrle et al., 2021).

The higher prevalence of cavity nesting birds in the GTR stands was also a significant finding (Fig. 5b). This guild is associated with large trees (Hobson and Bayne, 2000; Bunnell et al., 2002; Gutzat and Dormann, 2018), and is therefore disadvantaged by the intensive forestry practiced in Sweden (Carlsson et al., 1998; Imbeau et al., 2001; Andersson et al., 2018). Their association with large trees is among other factors related to fungal ecology (Remm and Lõhmus, 2011). Hence, a tree is suitable for the establishment or improvement of a nest cavity when the wood is softened by fungal infection (in particular for smaller birds). This process takes time and thereby favours hollow formation in larger older trees (Courbaud et al., 2022). Although we did not survey retained trees for the occurrence of cavities, it is reasonable to assume a higher prevalence of these structures in retained trees than in the production trees due to their older age and larger size (Larrieu et al., 2014; Courbaud et al., 2022). The average DBH of the retained trees in our study was 34 cm, and close to 10% of all retained trees were larger than 50 cm. This is very different from the control stands, in which the average DBH was 13 cm and no trees were larger than 50 cm.

The fact that woodpeckers, primary nest cavity producers, appeared in several GTR stands is a further indication of the importance of GTR for specialised bird guilds. Moreover, all four red-listed species encountered during the point count surveys are cavity nesters, three (black woodpecker, marsh tit and pied flycatcher) of which were only found in GTR stands, further indicating the importance of the large trees. Several of the broadleaf specialists and cavity nesters recorded, e.g. marsh tit, blue tit, pied flycatcher and nuthatch, were also associated with broadleaf GTR in a Swedish study done during the decade immediately following final felling (Söderström, 2009). In combination, these results highlight the likely benefit of broadleaf GTR to important bird guilds several decades into the rotation.

In contrast, birds that are associated with open land, and often found on recent clear-cuts, e.g. common whitethroat (*Sylvia communis*) and yellowhammer (*Emberiza citrinella*) (Söderström, 2009; Lindbladh et al., 2014b), were absent in the mid-aged production stands in our study, indicating a change in bird composition since the clear-cut phase. However, ground-nesting birds not associated with clear-cuts were frequently encountered (Table 1), and were significantly more common in the GTR stands than in the controls (Fig. 5c). This is perhaps due to a higher degree of heterogeneity in the former stands, as indicated by both the remote sensing data and the stand surveys (Table 2). We detected a larger difference in tree height within the GTR stands according to the remote sensing data, which was probably an effect of the retained trees, and may be a potential driver of the larger number of ground-nesting birds observed in GTR stands. Likewise, the larger DBH variation in the GTR stands according to the stand survey data could also result from retained trees affecting the growth rates of neighbouring production trees. In both cases, it indicates the GTR stand were more heterogenous regarding tree sizes, a factor often linked to higher bird diversity (MacArthur, 1964).

4.2. Species composition

The lack of a statistically significant difference in bird species composition between the stand types, as revealed by the NMS and multivariate analysis of variance (although close to significant, P = 0.054), as well as the direction of the observed difference in beta diversity, were in contrast to our expectations. Despite several bird species being unique to either the GTR (8 species) or control stands (2 species), there appeared to be simply too few such individuals to detect a significant difference in bird communities. Likewise, the higher beta diversity found across the control stands was unexpected, as the controls stands were structurally more homogeneous in several of the aspects assessed, relative to the GTR stands. We tentatively suggest that this effect may have been driven by GTR stands supporting a higher and less varying abundance of many overlapping species, and thereby providing limited opportunities for low population-size associated random turnover of species; as perhaps occurred in the control stands. However, as there was no clear difference between the stand types in the proportions of balanced turnover of species and changes in abundances this remains purely speculative.

4.3. Environmental drivers

Overall our results indicate a positive influence of the retained trees on bird diversity, but we were unable to tease out from the data readily interpretable drivers of these outcomes for bird abundance or composition. Furthermore, even though GTR stands had a higher overall bird species richness and abundance, and this enhanced diversity was reflected in multiple guilds expected *a priori* to benefit from retention trees, we could not provide deeper insights and quantify this benefit in relation to the number or basal area of retained trees. We can only suggest that the large variation among the GTR stands in terms of additional variables (e.g. species, size and age of trees retained which influence amount of tree related microhabitats cf. Asbeck et al. (2021)), regional bird species source pools, or territorial requirements of bird species, made it difficult to detect such relationships. In order to find a correlation and threshold values, i.e. to minimize random factors and noise, a larger number of stands with replicated amounts and species composition of GTR would likely be needed.

As discussed above, we argue that the significant variation in DBH and stand height is due to the retained trees, and it is probably one important driver behind the observed higher bird diversity in GTR stands. That said, there could be additional potentially important co-drivers to the retained trees that are also contributing to this pattern. For example, the abundance of CWD was higher in GTR than control stands. However, even in the GTR stands, the amounts (4.3 m^3 ha^{-1}) were an order of magnitude lower than in natural forest standards (Jönsson and Jonsson, 2007; Müller and Bütler, 2010), and also lower than national averages for all forests (9 m^3 ha^{-1}) (Nilsson et al., 2020). This challenges the potential importance of CWD as a quantified driver. In addition, the remote sensing data indicated a higher proportion of broadleaved trees in landscapes surroundings GTR stands, than in landscapes surrounding the controls (18% versus 13% broadleaves). Again, the difference was statistically significant but its biological importance is uncertain. That said, this may have increased the local pool of broadleaf bird species that could benefit from broadleaf GTR.

5. Future studies

The use of GTR in Sweden expanded during the early and mid-1990s, the time when the trees in our stands were retained. Our study thus provides a "glimpse into the future" as mid-rotation production stands with such old and large retained trees are unusual in today's landscape, but are expected to become more common in the decades to come. Our study thereby provides provisional support for the continued and future use of this practice, and indicates that the biodiversity contribution of retention trees continues to occur several decades into the stand's rotation. However, important questions remain to be answered. Despite the number of stands included in our study, the variation in the number trees retained, species composition of retained trees, and their environmental context within the stand (e.g. density and proximity of surrounding production trees), limited the capacity of our study to detect any threshold requirements for GTR, an important consideration for forest owners and managers. Studies in Central Europe have made efforts to find such thresholds for "habitat trees" to mitigate the effects of production forestry on organisms depending of structures provided by these trees (Bütler et al., 2013; Kebrle et al., 2021). Finding thresholds for retained trees could be possible in Sweden in the future when the pool of mid-aged stands with large, retained broadleaves have increased. Research is also needed on how to ensure the continued presence and optimized management of the individual trees retained during a rotation period, and after. These efforts go beyond simply ensuring that retained trees are not lost through time due to competition with surrounding fast growing production trees (Drobyshev et al., 2019; Rosenvald et al., 2019), but also that sufficient space is provided to create light environments under the canopy that will sustain the many photophilic species associated with broadleaf tree species (Koch Widerberg et al., 2012; Hedwall et al., 2019; Lariviere et al., 2021). The proximity, basal area, and height of surrounding production trees are aspects that have been investigated for other species groups such as wood-living beetles (Koch Widerberg et al., 2012), but not for birds. Therefore, this is an important additional area for future research.

CRediT authorship contribution statement

Matts Lindbladh: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Johan Elmberg:** Investigation, Writing – review & editing. **Per-Ola Hedwall:** Formal analysis, Writing – review & editing. **Emma Holmström:** Methodology, Writing – review & editing. **Adam Felton:** Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition.

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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