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Long-term effects of timber

harvest on cavity-nesting

birds in Norwegian boreal

forests

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Abstract

Fennoscandia is primarily covered in forests, but modern forestry has dramatically altered the landscape. Mixed-species and uneven-aged forests with natural gap rotations of 250 years were replaced by dense, even-aged stands that are clearcut every 80-120 years. Only 1.7% of productive boreal forest has never been clearcut in Norway, creating a patchwork of stands homogenized in structure, age, and composition. This transformation has removed niches and degraded habitats for myriad forest-dependent species. Deadwood- and cavity-dependent birds, insects, lichens, plants, and other taxa have been disproportionately threatened by the removal of standing dead trees (snags) in harvests and thinnings. Many cavity-nesting birds (hereafter cavity-nesters) have been deprived of their primary nesting and foraging cover.

I used a quasi-experimental approach to quantify changes in habitat variables and bird activity. Acoustic recorders were placed in 10 locations throughout southeastern Norway from 6 June to 22 July 2023. Each location contained a pair of forest sites – one that had been clearcut 40-80 years ago (CC) and one that had never been clearcut (NN). These sites are part of the EcoForest project (https://ecoforest.no/), a collaborative effort to study long-term changes in forest biodiversity caused by past forest management.

Automated analysis of all 3,026 h of audio recordings using BirdNET detected 169 bird species (<165 after validation). Neither total species richness nor Shannon diversity was higher in either SiteType (CC or NN), but diversity was more variable in NN. Far more recordings per day per site of excavators and old-growth icons were recorded in NN, while significant, marginally higher numbers were found for weak excavators and secondary nesters in CC. A declining keystone species, *Picoides tridactylus*, and an apex predator, *Accipiter gentilis*, were 7 and 9 times more frequently detected in NN, respectively.

NN had 1 more cavity per habitat survey plot (14/ha), habitat trees measuring 8 cm DBH larger on average, at least twice the total deadwood volume of CC, and trees with longer crowns. The homogenous conditions and scarcity of deadwood resources and cavities in CC likely prevent the recovery of numerous forest species. *Management Recommendations*: Converting up to half of even-aged to uneven-aged forestry to produce a true mosaic landscape of intensive plantations, extensive forests, and preserves will bolster resilience in populations, ecosystems, and the timber industry.

Keywords: bird, cavity, cavity-nester, deadwood, even-aged, forestry, snag, woodpecker

Introduction

The boreal forest of Fennoscandia covers >50 million ha in Norway, Sweden, and Finland (Esseen et al., 1997). Forestlands and wooded areas cover 14.2 million ha or 44% of Norway's land area. The majority (5.8 million ha) is coniferous forest dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), followed by silver- and downy birch (Betula pendula and B. pubescens) forests (4.2 million ha) and mixed-species forests (2.1 million ha) (Fjellstad & Skrøppa, 2020). Scandinavian forestry is highly efficient at producing timber by using rotation ages of around 60-100 years, heavy machinery, and cutting 45%, 70%, or 85% of the annual growth increment in Norway, Finland, and Sweden, respectively as of 2010. The natural "rotation age" of gaps in old-growth spruce is around 250 years, but modern spruce forests are capped at under half this age (Caron et al., 2009). Nearly all productive forest is under intensive, plantation-style management for Norway spruce (hereafter spruce) or Scots pine (hereafter pine) while less than 5% of all forestland is protected in the region (Gustafsson et al., 2010). Most productive forest has been clearcut at least once, and a mere 1.7% has not been clearcut (Asplund et al., 2024). This drastic shift has created a new forest landscape that is much denser, darker, and younger. The homogenization and degradation of habitat quality at such a large results in forest-dwelling species comprising 50% of all threatened and endangered species in Norway, and cavitydependent species are disproportionately threatened (Andersson et al., 2017, Norwegian Biodiversity Information Centre, 2021). Many of these red-listed species cannot live without old trees, deadwood, or snags for food and cover (Thorn et al., 2020).

Snags are standing dead trees that form much of the basis for the saproxylic community, meaning taxa that rely on dead and decaying wood. Many birds rely on snags and damaged, dying, or senescent trees for nesting and roosting. For decades, snags have been known to provide habitat for hundreds of species as they progress through decay stages. However, ecologically valuable deadwood has been systematically removed from forests during silvicultural operations (Thomas et al., 1979, Thorn et al., 2020).

Cavity nesters either require or prefer holes in trees and snags for raising their young. Primary cavity nesters, or excavators, most commonly chisel out a hole in a snag or dead branch (Andersson et al., 2017, Cockle et al., 2011, Thomas et al., 1979). Weak excavators can only expand a natural or woodpecker-made cavity or excavate in already well-rotted, soft wood. Secondary cavity nesters cannot create cavities, but often inhabit cavities made by the previous two groups. Many birds prefer the cavities for their safety from predators and the elements, with larger snags supporting larger woodpeckers and further enhanced microclimate control (Bütler et al., 2024, Conner et al., 1975, Hågvar et al., 1990).

Woodpeckers are commonly the only strong excavators in the ecosystem because they alone can withstand the rigor of pecking wide, deep holes with their powerful beaks. Most will take advantage of wood that is already rotting or damaged by fungi, but exceptionally strong species such as *Dryocopus martius* (Black Woodpecker) can bore into live trees. Woodpeckers almost always create and use a new cavity each year, thus allowing numerous other birds, mammals, insects, fungi, etc. to inhabit the old cavity. Although not usually described as such, woodpeckers are apex predators in the saproxylic food web and control populations of many wood-boring insect pests (Andersson et al., 2017, Cockle et al., 2011, Thomas et al., 1979).

I used a quasi-experimental approach to quantify the long-term effects of clearcutting in the boreal forest by analyzing changes in habitat variables and bird activity. Acoustic recorders were placed in 10 locations throughout southeastern Norway from 6 June to 22 July 2023. Each location contained a pair of forest sites—one that had been clearcut 40-80 years ago (CC) and one that had never been clearcut (NN). These sites are part of the EcoForest project (https://ecoforest.no/), a collaborative effort to study long-term changes in forest attributes (e.g., litter decomposition and biodiversity) caused by past forest management.

My research focuses on cavity nesters and their habitat. I hypothesize that

- 1. NN have a greater abundance of snags, cavities, volume of standing deadwood, and crown length. CC have greater slenderness because of higher stand density.
- 2. The overall bird community will change between NN and CC.
- 3. Cavity nesters will be represented in NN with a higher abundance of calls.
- 4. CC are more homogeneous and NN are more varied among themselves in terms of bird diversity and habitat metrics.

Methods

Study Site

The EcoForest project (<u>https://ecoforest.no/)</u> is a collaborative effort between universities, the Norwegian government, and private organizations in Norway to research the long-term effects of clearcutting on forest communities and processes (Asplund et al., 2024).

Researchers in the EcoForest (EF) project found 12 locations of boreal forest stands in southeastern Norway (Fig. 1) that contain a pair of Sites: a clearcut Site (hereafter CC) that has regrown to 40-80 years old after one rotation of clearcutting vs. a near-natural Site (hereafter NN) that has developed without clearcutting. The two Sites within each location were selected due to having similar soil, tree cover, and other factors to isolate the effect of the harvest regime. Researchers have collected and analyzed data on numerous habitat metrics including soil carbon fluxes, insect diversity and abundance, and litter decomposition within 15m x 15m plots (Asplund et al., 2024). We used these plots as a starting point to categorize the forests in this study. With a limited number of acoustic recorders (hereafter detectors), EF10 and EF1 were removed from our search effort due to travel constraints and their similarity to EF12 and EF2. My study area covers 10 locations, or 10 CC and 10 NN.

The locations and sites are hierarchically ordered. Coordinates were recorded on a Garmin GPSMAP 64st GPS unit with 3 m accuracy and labeled with the following naming convention: EF for EcoForest, the location number, and CC or NN for SiteType.

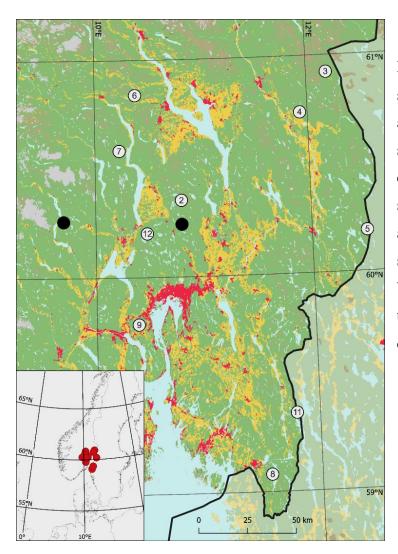


Fig. 1. The 10 study locations span 59.079766°N-60.921114°N and 11.546541°E-12.188859°E in southeastern Norway. Each is comprised of a mature even-aged stand (CC) and mature unevenaged stand (NN) of *Picea abies* spruce forest. Note that EF10 (far West) and EF1 were omitted from this study due to our supply of 20 detectors.

Acoustics

In the Field

Bat detectors were placed within 20 m of the EF plot boundary, and bird detectors were placed within 10 m of the bat detector. Bird detectors (SM4, Wildlife Acoustics) were strapped to a tree that faced a clearing and had no overhanging branches when possible. One of the dual microphones faced the forest interior as the other faced the clearing.

The detectors were deployed, maintained, and retrieved in the same order to provide the same amount of recording opportunity. We started with the southeasternmost location and advanced clockwise. The first was deployed on 5 June 2023, and the last was retrieved on 23 July 2023. Each detector had around 3 weeks of recording time before and after maintenance. All data from the SD cards were loaded into a central database.

Processing Acoustic Data

All raw, 10-min audio recordings were identified to species with BirdNET Lite (hereafter BirdNET) (https://github.com/kahst/BirdNET-Lite). BirdNET is a neural network that identifies the most likely bird species calling in each 3-sec audio clip of an audio file (Kahl et al., 2021). The top identification is given a confidence score in the output. The entire dataset of 3,026 h was fed into BirdNET for analysis. Each Site took ~1 h to process through BirdNET with default settings except for the following: batch (3), threads (16-20), minimum confidence (0.6), and location (0.01) threshold. The BirdNET default species list was used for the average of all locations (60.23663° N, 11.21735° E) for all weeks of the year for a total of 294 possible species. The outputs were fed into R for data wrangling and statistical analysis (R Core Team 2023).

After receiving and compiling all the outputs from BirdNET, I began the validation process. Ideally, researchers listen to 100 samples of high-confidence (minimum confidence ~0.6) recordings for every species detected by BirdNET, judge whether these are correct, and weed out the false positives (Ware et al., 2023). Due to time and personnel constraints, I focused efforts on my focal taxa of cavity-nesters (Appendix Fig. A1) and old-growth icons, meaning species that are common in or characteristic of old-growth spruce forests in Fennoscandia. All validated species are listed in Appendix Fig. A2.

For each focal species, I randomly sampled 100 output files without replacement (or all output files if n < 100). I identified whether the top-ranked bird was present in each 3-sec clip and labeled the file using the following format: clip*n*.SpeciesCode.T/F/U_clip-n+1.SpeciesCode... The annotation 1.CERFAM.T translates to the first clip of the current 10-min audio recording, BirdNET's ID of *Certhia familiaris*, and True for my judgement of the 3-sec clip. I compiled a .csv file containing all sample outputs to efficiently track which audio file, clip number, starting time within the 10-minute audio file, species, and validation result applied to each output. BirdNET's accuracy with "error bars" was calculated as $\frac{T \pm U}{n}$, where T = true identification, U = unknown identification that could not be confirmed nor denied, and n = total samples for that species.

Habitat Survey

The habitat survey estimated the abundance and diversity of local nesting and roosting opportunities for birds and bats. A 15 m fixed-radius circle point count was centered on the midpoint between the bird and bat detectors. A 20 m measuring tape was used to identify the center point, which stems are inside the plot, and to divide the circle into manageable portions. Every tree and snag (standing dead tree) over 10 cm (~4 in) in diameter at breast height (DBH; 1.37m or 4.5ft) within the plot were observed with the naked eye and binoculars from at least 3 vantage points. The following variables were recorded for all stems: a unique ID number in the form of TR## for trees and SN## for snags, distance from centroid (point M), decay stage (1-7), presence of a broken top (T/F), DBH (to nearest mm), cavities (count), loose bark (T/F), large dead branches (count), and bird foraging or nesting signs were recorded for all stems within or intersecting the circle. Broadleaf count is the total number of deciduous stems found per site.

Functional Definitions

Decay stage follows the standard scale used in Thomas et al. (1979) where 1 and 2 are live trees and 3-7 are snags. Stages 8-9 are considered downed woody debris and therefore omitted from the survey. The presence of a broken top means the central leader has been snapped off past the most recently grown whorl of twigs and would invite decay into the stem. A cavity (code = C) is a hole located in a tree or snag and is large enough to be used by the smallest secondary nester, *Troglodytes troglodytes* (Eurasian wren). The cavity must not face so far up as to collect water or down as to cause nest material to fall out. Dead branches (code = DB) include dead leaders on live trees, intact branches, and branch stubs that are

large enough for a *Dendrocopos minor* (lesser spotted woodpecker) to excavate a nest site. The branches provide enough depth for a nest cavity. Loose bark (code = LB) refers to patches of external bark that are beginning to slough off the stem. Loose bark was recorded if it could shelter a roosting bat or harbor a *Certhia familiaris* (treecreeper) nest. Treecreepers prefer long patches close to the stem (Harrap, 2015).

EcoForest Habitat Variables

I tested multiple variables from Asplund et al. (2024) to analyze habitat differences and their explanatory power on bird calls (Table 1). Standing deadwood volume = total volume of snags (m³ha⁻¹). Total deadwood = total volume of snags + downed woody debris (m³ha⁻¹). Total volume per living volume = $\frac{total \, deadwood \, volume \, (m^3ha^{-1})}{total \, livewood \, volume \, (m^3ha^{-1})}$. Crown length = $\frac{height_{tree}}{DBH}$, where height and DBH are measured in cm.

Table 1. Generalized linear mixed models using 3 metrics from (Asplund et al., 2024) and 3 habitat survey counts. \dagger = zero-inflated model, * = interaction. Red represents results not in the final model picked using AIC.

Calls/site	Habitat variable	Best model + (1 Location/Site)	χ2	р	χ2*	p*	df
Excavators	SiteType	Species * SiteType	3.65	0.06	19.72	0.00	17
Excavators	Standing Deadwood vol.	Species + Standing Deadwood vol.	7.19	0.01	7.67	0.26	17
Excavators	Crown Length	Species * Crown Length	0.12	0.73	10.56	0.10	17
Excavators	Slenderness	†Species * Slenderness	10.13	0.00	22.40	0.00	18
Excavators	Cavity count	Species * Cavities	0.02	0.90	11.85	0.07	17
Excavators	Broadleaf count	Species + Broadleaf	0.24	0.62	8.97	0.18	11
Excavators	Snag count	†Species * Snags	0.16	0.69	12.48	0.05	18
Weak excavators	SiteType	Species	NA	NA	1.09	0.58	6
Weak excavators	Standing Deadwood vol.	Species	NA	NA	1.59	0.45	6
Weak excavators	Crown Length	Species * Crown Length	5.62	0.02	11.90	0.00	9
Weak excavators	Slenderness	Species * Slenderness	3.52	0.06	5.86	0.05	9
Weak excavators	Cavity count	Species * Cavities	1.01	0.32	8.42	0.01	9
Weak excavators	Broadleaf count	Species	NA	NA	1.68	0.43	6
Weak excavators	Snag count	Species	NA	NA	0.89	0.64	6
Secondary	SiteType	Species * SiteType	14.27	0.00	42.56	0.00	41
Secondary	Standing Deadwood vol.	Species (AIC); Species + Standing Deadwood vol. (p)	6.03	0.01	24.25	0.15	22
Secondary	Crown Length	Species * Crown Length	7.55	0.01	43.57	0.00	41
Secondary	Slenderness	Species * Slenderness	0.50	0.48	59.39	0.00	41
Secondary	Cavity count	Species + Cavities	5.37	0.02	7.48	0.99	23
Secondary	Broadleaf count	Species (AIC); Species * Broadleaf (p)	7.38	0.01	30.01	0.04	22
Secondary	Snag count	Species + Snags (AIC); Species * Snags (p)	26.15	0.00	29.63	0.04	24

Statistical Tests

All tests were conducted in R (R Core Team 2023). Calls were aggregated per Day per Site per Location in negative binomial GLMMs (hereafter NegBin) or zero-inflated NegBin in the *glmmTMB* package (Brooks et al., 2017). To test if bird activity differed between the two SiteTypes (CC and NN), Species, and if Species influenced the difference between SiteTypes, I fitted NegBin and negative binomial distribution of errors with the count of calls as the

response variable. Explanatory variables included SiteType, Species, SiteType × Species interaction, and others with their formulas shown in Table 1. Site nested in Location was included as a random intercept. I used the R package *DHARMa* for model validation, i.e., to check that the statistical model fitted the data (Hartig & Lohse, 2022). The same aggregation was used for pairwise Wilcoxon signed rank, t-, and F-tests for all bird taxa for median, mean, and variance in number of calls recorded, respectively. Habitat variables from our habitat survey and Asplund et al. (2024) were aggregated to Site, as these were only recorded once. PERMANOVA testing with the *vegan* and *prabclus* packages was conducted on the entire bird community using a matrix of total records per species per Site/Location and presence/absence per species per Site/Location (Hennig & Hausdorf, 2023, Oksanen et al., 2022).

Results

Acoustic Data Collection

The bird recordings ranged from 21-37GB (average 27.1). A total of 181,570 min (3,026 h) of recordings were retrieved from bird detectors. The first half of recordings at EF8-CC-A was lost due to an error in the field.

Habitat Variables

Tree/Snag Metrics

Recorded trees and snags in NN sites were on average 8 cm DBH larger (Linear regression: t = 6.5, p < 0.001, df = 3). Species-specific linear models were only significant for spruce, with the average spruce in NN being 8.6 cm larger (Linear regression: t = 6.3, p < 0.001, df = 3) (Table 2). Snag counts did not differ. Only snags in decay stages 1-2 were definitively more variable in CC (sd = 2.0 vs. 5.8, F-test: F = 8.4, p = 0.004), but snags in stage 3-4 tended to be so (sd = 4.1 vs. 7.4, F = 3.2159, p = 0.097).

Table 2.	Regression	n models or	n cavities	and DBH	for habitat	trees in	the habitat	survey.

Response	Regression type	Formula (CC vs NN)	Estimate	Test stat	р
Cavities	Poisson	cavities ~ SiteType	1.17	2.73	0.006
Cavities Birch	Poisson	cavities ~ SiteType	1.27	2.45	0.014
Cavities Spruce	Poisson	cavities ~ SiteType	1.32	1.67	0.095
DBH	Simple linear	dbh ~ SiteType	8.33	6.53	< 0.001
DBH Spruce	Simple linear	dbh ~ SiteType	8.63	6.26	< 0.001

Table 3. Counts of microhabitat features taken during the habitat survey on each 15m circle plot centered on the midpoint of bird and bat detectors in each Site. Species are *Betula pendula* and *B. pubescens* (birch), *Picea abies* (spruce), and *Pinus sylvestris* (pine). **D**iameter at **B**reast **H**eight is presented as mean \pm standard deviation. Loose bark is a count of trees with at least one suitable patch present. Remaining responses are counts.

Site Type	Species	DBH (cm)	Cavities	Loose bark	Dead branches	Trees/ Snags
NN	Birch	24.35 ± 10.37	15	6	7	11
$\sqrt{7}$	Spruce	27.45 ± 12.27	8	60	14	109
	Pine	32.13 ± 6.12	0	1	2	3
CC	Birch	18.75 ± 5.36	5	5	7	13
	Spruce	18.81 ± 6.82	2	45	9	102
	Pine	38	0	0	1	1

All microhabitat features were present in greater numbers in NN, except for an equal number of dead branches in birch and 0 cavities in pine (Table 3). All snags and only those living trees with cavities, loose bark, dead branches, or broken tops were inventoried. Poisson regression revealed 1 more cavity per $706.5m^2$ (15m circle plot) in NN sites (z = 2.733, p = 0.006, df = 2), translating to 14 more cavities per ha of NN forest (Table 2). The same trend held for birches (z = 2.451, p = 0.014, df = 2) and tended to for spruces (z = 1.670, p = 0.095, df = 2).

Forest-wide Metrics

Neither the mean nor maximum age overlapped between SiteTypes, making age a confounding variable. CC appear to have a nearly 1:1 relationship with mean and maximum age, while NN are far more variable (Fig. 2). NN's average age is twice as old (128 vs 64 years, Paired t-test: t = -13, p < 0.001) and tended to be more variable (sd = 22 vs.12, p = 0.093). The same is true for maximum age (255 vs. 89 years, t = -11, p < 0.001) and its variance (sd = 36 vs. 14, p = 0.013).

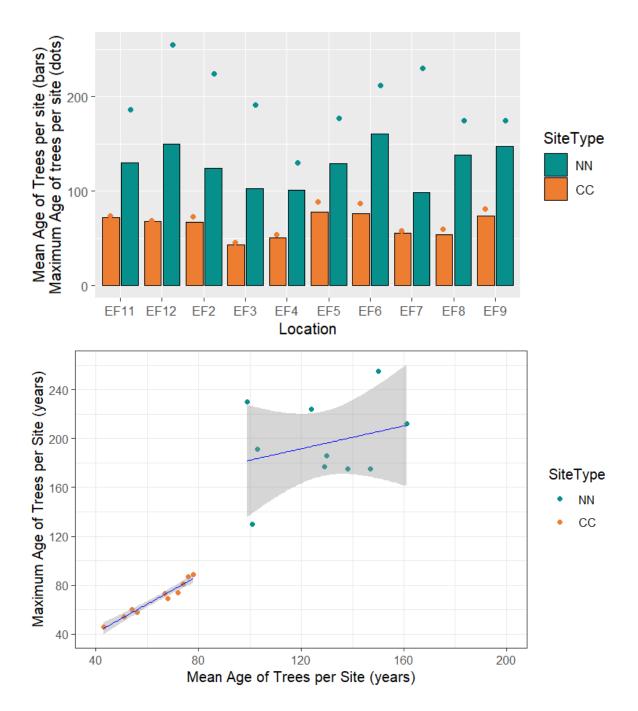


Fig. 2. Mean age of the 5 largest trees (bars) and age of the oldest tree (dots) for each Site and Location of regrown clearcut (CC) and near-natural (NN) SiteType (top). Maximum age vs. mean age by Site presented with trendlines and 95% confidence intervals (bottom). Raw data from Asplund et al. (2024).

The median and mean crown lengths tended to be longer in NN (V = 10, p = 0.083; t = - 1.943, p= 0.084). Trees in CC had higher median and mean scores for slenderness, meaning a tree of a given height is thinner in CC (V = 52, p = 0.010; t = 3.5253, p=0.006).

Despite the habitat survey finding no differences in snag count, EcoForest data suggests the median volume of standing deadwood (a.k.a. snags) was likely twofold greater in NN (16.3

 $m^{3}ha^{-1}$; V = 9, p = 0.064, Fig. 3). NN had triple the median total (standing and downed) deadwood volume (53.6 $m^{3}ha^{-1}$, V = 2, p = 0.006) and variance (sd = 55.1, F = 0.142, p = 0.008). CC's median ratio between the total volume of deadwood to the total volume of livewood was a quarter of NN's (median(CC) = 0.037, V = 4, p = 0.014). CC is more homogeneous with a fifth of the variance (sd = 0.05, F = 0.031, p < 0.001). NN provide far greater deadood volumes, around 15% of the volume of the livewood, and snags are larger but not more abundant.

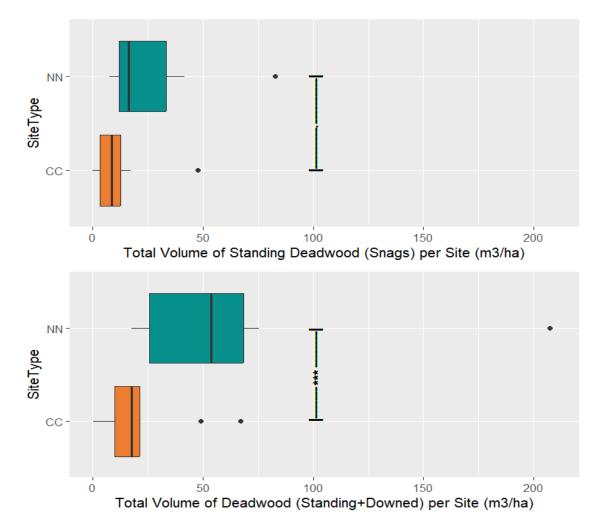


Fig. 3. Distribution of deadwood resources (m^3ha^{-1}) per regrown clearcut (CC) and nearnatural (NN) SiteTypes. Dot (.) = p < 0.1, asterisks (***) = p < 0.001. Raw data from Asplund et al. (2024).

Birds

Whole Bird Community

BirdNet identified 169 bird species overall with 14 unique to CC (n = 52 records) and 12 to NN (n = 16 records). A total of 237,459 BirdNET outputs were generated encompassing 198 h of target recordings (15.3% of total recording time).

One species with only one record, *Zapornia pusilla* (Ballion's Crake), was removed as a complete false positive due to not being listed as occurring in or extirpated from Norway (BirdLife Norge 2022). *Corvus corone* (Carrion Crow) was misidentified in all 19 records and was re-coded as *Corvus cornix* (Hooded Crow). The most recorded species were all secondary nester passerines, with *Regulus regulus* (Goldcrest) as the most-recorded bird (Table 4). All woodpeckers and weak excavators were present in both site types. Secondary nester richness was unaffected by SiteType.

Table 4. Top 5 species with the most abundant recordings for regrown clearcut (CC) and nearnatural (NN) SiteTypes. Only records from the 5 most numerous species for each Site are presented – blanks do not represent 0 records.

Scientific name	Common name	CC	NN
Regulus regulus	Goldcrest	17284	26556
Erithacus rubecula	European Robin	12263	
Fringilla coelebs	Common Chaffinch	8415	9028
Muscicapa striata	Spotted Flycatcher	7084	
Certhia familiaris	Eurasian Treecreeper	6405	7571
Troglodytes troglodytes	Eurasian Wren		17594
Spinus spinus	Eurasian Siskin		7529

The overall bird community composition did not differ between SiteTypes (PERMANOVA: $F_{1.18} = 0.79$, p = 0.67), but rather among Locations ($F_{1.18} = 0.79$, p = 0.67). The community composition changed by Site with PERMANOVA testing on the presence/absence matrix aggregated to Site (F = 1.38, p = 0.018). Species richness was not greater in either SiteType but was more variable in NN (sd = 9.4 vs. 8.1, F = 0.74, p = 0.001) (Fig. 4).

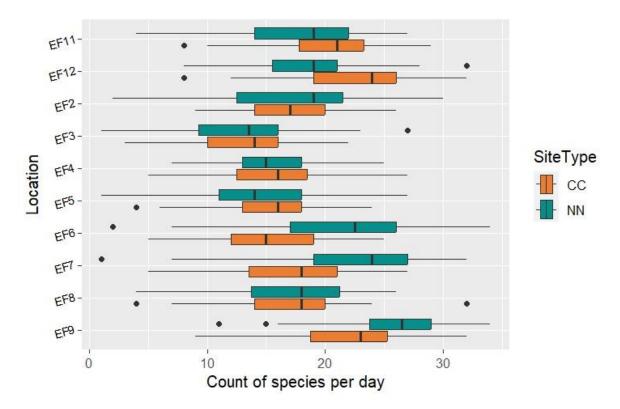


Fig. 4. Distribution of species richness counted by each detector per day per Site for each regrown clearcut (CC) and near-natural (NN) SiteType.

The median Shannon Diversity Index for NN (2.74 ± 0.62) was three times more variable than CC (2.69 ± 0.22 , F = 0.12, p = 0.005), however the variability was influenced by one NN with low diversity (Fig. 5).

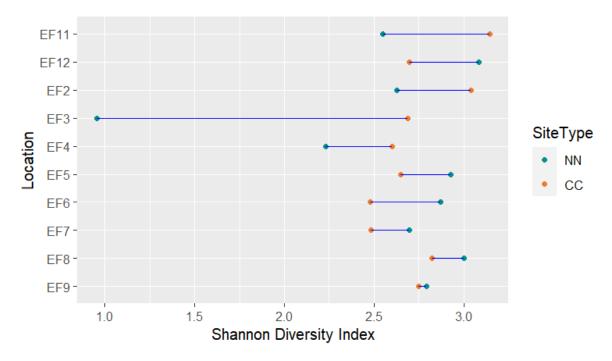


Fig. 5. Shannon Diversity Index on the entire bird community for each pair of Sites within each Location in regrown clearcut (CC) and near-natural (NN) SiteTypes.

Cavity Nesting Guilds Strong Excavators (Woodpeckers)

Every species of woodpecker had more recordings in NN sites except *Picus viridus* (Green Woodpecker). and *Dryocopus martius* (Black Woodpecker) with no preference. NN had 88% of *Piciodes tridactylus* (Eurasian Three-toed Woodpecker) and 95% of all *Dryobates minor* (Lesser Spotted Woodpecker) calls (Fig. 6). The strong excavator guild is extremely skewed towards NN by median count (V = 126273, p < 0.001). Standing deadwood (negative binomial GLMM: $\chi^2 = 7.1892$, p = 0.0073, df = 17) and likely the NN SiteType ($\chi^2 = 3.6521$, p = 0.0560, df = 17) positively predict woodpecker calls. Slenderness had the opposite effect (zero-inflated negative binomial GLMM: $\chi^2 = 10.1313$, p = 0.0015, df = 18).

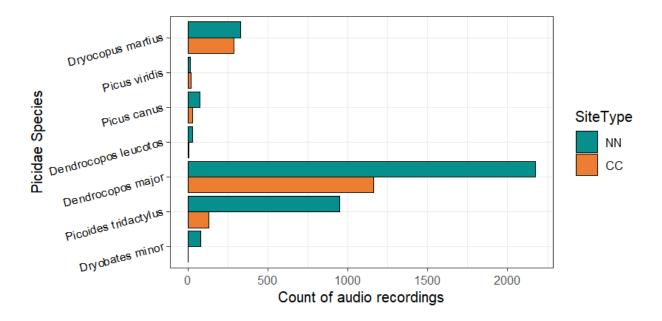


Fig. 6. Total count of records identified to woodpecker species in regrown clearcut (CC) and near-natural sites (NN).

Weak excavators

The weak excavator guild is likely more active in CC (V = 70509, p = 0.057) (Table 1). The count of weak excavator calls was negatively correlated with crown length ($\chi^2 = 5.6$, p = 0.018, df = 9) and likely positively correlated with slenderness ($\chi^2 = 3.5196$, p = 0.061, df = 9) in NegBin. More activity is found where the trees are thinner per unit height and do not have branches far down the stem.

Secondary Nesters

Records of secondary nesters were negatively correlated with NN ($\chi^2 = 14.2740$, p = 0.0002, df = 41) and crown length ($\chi^2 = 7.6$ p = 0.0060, df = 41). Cavities ($\chi^2 = 5.3674$, p = 0.021, df

= 23), and snags (χ^2 = 26.1467, p < 0.0001, df = 24) had a negative trend, but issues such as balancing the dataset and model fit make conclusions uncertain.

Other Birds of Interest

Both *Aegolius funereus* (Boreal Owl) and *Strix aluco* (Tawny Owl) were found nine and two times more in CC, respectively, while *Glaucidium passerinum* (Eurasian Pygmy-owl) calls were six times more numerous in NN (Fig. 7). *Strix uralensis* (Ural owl) was one of the top 3 most-recorded birds for multiple sites, but its accuracy was highly questionable at under 10%.

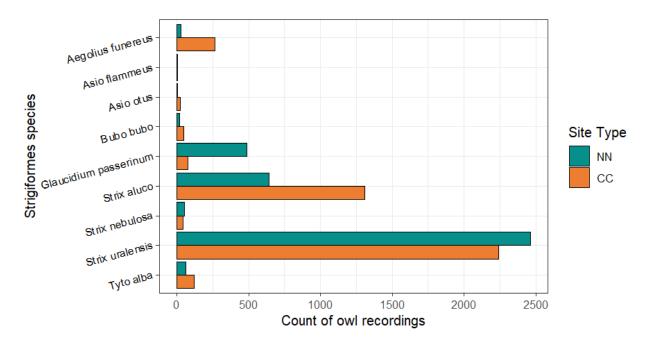


Fig. 7. Total count of records identified to owl species in mature, regrown clearcut sites (CC) and uneven-aged, near-natural sites (NN).

Old-growth icon calls were 1.4 times more common in NN (V = 1069718, p < 0.0001). Records for three species were more than sevenfold greater in NN, but *Pinicola enucleator* (pine grosbeak) was an accurately estimated species with a reversed trend (Table 5). Table 5. Count of records for old-growth icons, meaning species considered to be characteristic of old-growth boreal spruce forests in Fennoscandia (Virkkala & Rajasärkkä, 2006). Birds with a "-" sign have been removed from analysis due to other species with similar calls being more likely in the region. BL = average body length taken from (Svensson et al., 2021). Column n represents the number of calls per regrown clearcut (CC, orange) and near-natural (NN, turquoise) SiteType. Column NN/CC represents the ratio of calls for NN and CC, with higher values being *x* times more common in NN.

Nester type	BL (cm)	Scientific name	Common name	n	$\frac{NN}{CC}$
Excavator	43	Dryocopus martius	Black Woodpecker	328 288	1.14
Excavator	24.5	Dendrocopos major	Great Spotted Woodpecker	2176 1162	1.87
Excavator	22.8	Picoides tridactylus	Eurasian Three-toed Woodpecker	950	7.2
Weak excavator	11.3	Lophophanes cristatus	Crested Tit	132 2211	0.95
Secondary	13.8	Phoenicurus phoenicurus	Common Redstart	2325 3074 351	8.76
Secondary	13.5	-Tarsiger cyanurus	Red-flanked Bluetail	29 80	0.36
Secondary	13.3	Certhia familiaris	Eurasian Treecreeper	7571 6405	1.18
Secondary	13.3	-Poecile cinctus	Gray-headed Chickadee	11 16	0.69
Secondary	11.5	Ficedula parva	Red-breasted Flycatcher	3547 3474	1.02
Non-cavity	82	Tetrao urogallus	Western Capercaillie	135 91	1.48
Non-cavity	52.5	Accipiter gentilis	Northern Goshawk	287 31	9.26
Non-cavity	27.5	Perisoreus infaustus	Siberian Jay	6 6	1
Non-cavity	27.5	Turdus viscivorus	Mistle Thrush	854 936	0.91
Non-cavity	20.5	Pinicola enucleator	Pine Grosbeak	27 34	0.79
Non-cavity	10	-Phylloscopus trochiloides	Greenish Warbler	3 2	1.5

BirdNET Validated

During manual validation of 37 cavity nesters and old-growth icons, 3 species were removed as their calls were most likely confused with those of other species more likely to be in the study area: Poecile cinctus (n = 27), Phylloscopus trochiloides (n = 5), and Tarsiger cyanurus (n = 109). The total true number of species detected is most likely under 165. Manual validation of these 34 focal species yielded variable accuracy ratings for nester types (Fig. 8). The median accuracy for these 34 species was 95%, while the mean was $75\% (\pm 33\%)$ (Appendix Fig. A2). Four of five non-cavity nesters were $\geq 80\%$ correct, but the guild was skewed by Tetrao urogallus (Wester Capercaillie) at 12-16% accuracy. Within strong and weak excavators, Dendrocopos leucotos (White-backed Woodpecker) was very uncertain due to many IDs appearing around Picoides tridactylus (Three-toed Woodpecker) calls, with the latter being more likely (Fig. 9). Dryobates minor (Lesser Spotted Woodpecker) was only 16-21% accurate due to the similarity of its drumming to wood creaking in the wind or rain. Secondary nesters ranged from 0-6% at worst for Bubo bubo (Eurasian Eagle Owl) and 100% at best for multiple passerines (Fig. 10). Passerines had a mean accuracy of 96%, with the lowest being 68% for Ficedula parva (Red-breasted Flycatcher). Conversely, most owl calls were recordings of cows, cowbells, airplanes, wind, and sheep.

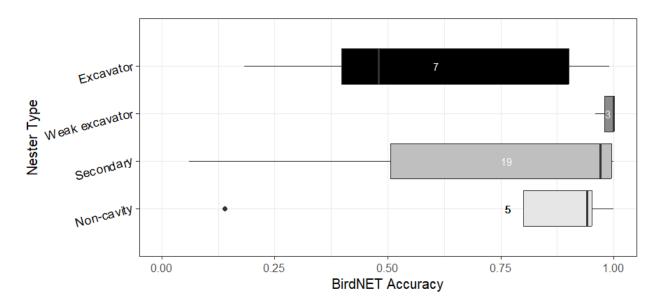


Fig. 8. Boxplot of BirdNET's accuracy rating for manual validation of 34 species organized by nester type. Numbers represent n and are located at the mean of each nester type's distribution.

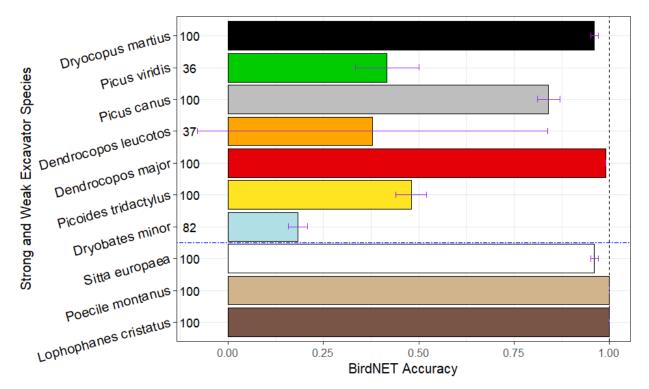


Fig. 9. BirdNET's accuracy rating for manual validation of all 7 woodpecker species (above the dashed line) and all 3 weak excavators. Purple "error bars" represent accuracy \pm results that were unable to be confirmed or denied as the species identified by BirdNET.

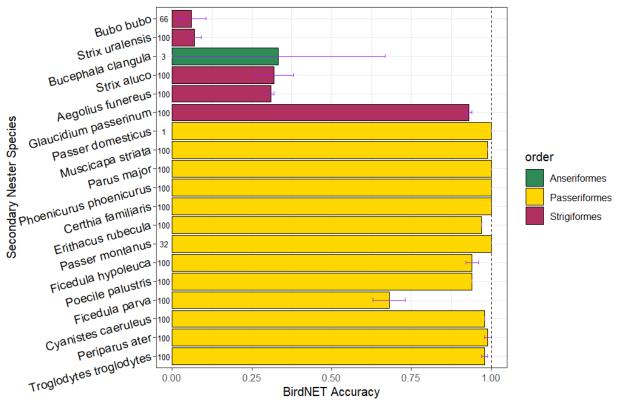


Fig. 10. Manual validation results for BirdNET's accuracy rating of 19 secondary cavity nester species organized by order and body length. Note very low accuracy for owls (except *Glaucidium passerinum*) Note *Bucephala clangula* had only one record each for True, False, and Unknown.

Discussion

Forestry

Plantation forestry is highly valuable for timber production, but it comes at the cost of forming an even-aged, monotypic, structurally homogeneous stand. Dying trees and snags are traditionally removed in thinning to free up light, nutrients, and growing space for the crop trees. The lack of niches, older trees, snags, and deadwood simplifies the ecosystem and reduces its capacity to support a variety of species. Many of the losing species are now threatened and endangered. The single best estimator of the abundance and diversity of species of conservation concern is habitat heterogeneity. The best resource predictor is deadwood volume, which should be over 21 m³ha⁻¹ for red-listed species (Hekkala et al., 2023). This threshold is reached in 9/10 NN but only 3/10 CC. The mean NN standing volume is already more than enough at 25.7m³ha⁻¹, with a median total volume of 53.67m³ha⁻¹.

Species that require open spaces benefit from disturbance and are more abundant in evenaged retention harvests and younger forests (Viljur et al., 2022). At the same time, much or all habitat quality, depending on the species, is lost for forest dwellers during the dense and dark stem exclusion phase. Mature even-aged forests can provide good habitat for forestdependent species as well, but usually only after 80 years. Less than two decades of suitable habitat are left in every rotation of 90-100 years, while uneven-aged forestry mimicking natural gap disturbances would keep most of the stand intact (Kuuluvainen et al., 2021). All groups that depend on the forest can be sustained and even enhanced with responsible management. Forestry that benefits humans, other animals, and plants cannot be achieved when one type of forest management becomes functionally the only type left on the landscape.

Birds

Norway has fewer than 10% of the number of even-aged forest studies than Finland and Sweden, but the entire Fennoscandian region lacks practical information on how forestry in general affects birds. Arguably the most visible group of forest-dwellers (besides trees) has been included in fewer studies than the following taxa, in descending order of the number of studies: arthropods in general, beetles, vascular plants, fungi, lichens, and mammals (Savilaakso et al., 2021). There is a severe lack of information in a region that is home to hundreds of bird species, and I hope this study helps to fill in some gaps.

The lack of a trend for Shannon diversity, species richness, and call abundance for the entire bird community between SiteTypes is not unexpected when considering the scale of the study. Each pair of Sites was selected to be as similar as possible, save management history, so the vast majority of species would be expected in both SiteTypes. Distances to mires and wetlands can make some Locations much more likely to receive shorebirds and waterfowl than others, regardless of SiteType. The greater overall abundance of calls in NN was expected as these older stands contain far greater structural variation and thus niches than CC. This complexity would harbor a greater variety of prey species and may sustain populations better during times of stress.

Woodpeckers create the vast majority of cavities in the boreal region, especially in areas without many deciduous trees (Andersson et al., 2017). Aspen is an extremely valuable resource for cavity nesters in spruce forests (Hågvar et al., 1990). Aspen is the favorite or 2nd favorite nest tree of all Fennoscandian woodpeckers (Table 6) and harbored 90% of cavity sites even in forests composed of only 10-15% aspen (Pakkala et al., 2024). Increasing the proportion of the most sought-after nest tree to 5-10% canopy cover should aid woodpecker recovery. Woodpeckers produced 5.7 cavities km⁻²year⁻¹ in natural forests, but only 1.5 in plantation forestry of monotypic spruce. Excavation rates were similar for each bird species and within each tree species or health class. The current forest landscape of structurally homogeneous stands of one conifer, usually harvested within 100 years, limits cavity production by decay and by woodpeckers. These conditions may cause a shortage of these high-quality nest sites and corresponding saproxylic insects, resulting in a cascade of populations shrinking (Pakkala et al., 2024).

Table 6. All strong primary cavity nesters (excavators) with % nests found per tree species. Tree species with <10% of total nests are omitted. Note *Dendrocopos major* is listed as 'generalist' due to \leq 5 nests per species in spruce (*Picea abies*), pine (*Pinus sylvestris*), alder (*Alnus sp.*), oak (*Quercus sp.*), and rowan (*Sorbus acuparia*). Data from Hågvar et al. (1990).

BL (cm)	Species	English	Norwegian	% nests by tree species
43	Dryocopus martius	black woodpecker	svartspett	Populus tremula (66%)
				Pinus sylvestris (32%)
33	Picus viridis	green woodpecker	grønnspett	Populus tremula (88%)
29.5	Picus canus	grey woodpecker	gråspett	Populus tremula (91%)
26.5	Dendrocopos leucotos	white-backed	hvitryggspett	Betula sp. (45%)
		woodpecker		Populus tremula (36%)
24.5	Dendrocopos major	great spotted	flaggspett	Populus tremula (78%)
		woodpecker		Betula sp. (12%)
				generalist
22.75	Picioides tridactlyus	three-toed	tretåspett	Picea abies (69%)
		woodpecker		Populus tremula (31%)
15.25	Dendrocopos minor	lesser spotted	dvergspett	Populus tremula (40%)
		woodpecker		Betula sp. (34%)
				Alnus sp. (26%)

Weak excavators tended to be more active with greater slenderness and lower crown length, both of which are very common for trees in the stem exclusion phase and densely stocked stands (Oliver & Larson, 1995). However, the group did not react cohesively to some variables. For example, each member tended towards a positive, negative, or lack of a relationship with cavities (Wald Chi-square Test on species * cavities interaction: $\chi^2 = 8.4$, p = 0.015, df = 9).

Many secondary nesters will use cavities facultatively instead of as an obligatory criterion for nesting. Although secondary nesters had no significant trend with cavity count, the reduction of high-quality nest sites may cap the maximum population in the future rather than limit it currently. The hegemony of intensive forestry is a reasonable explanation for my results, the continued decline of species today, and the range reductions and population crashes of numerous birds since the start of widespread Scandinavian forestry in the 1940s and '50s.

My results by nesting guild are robust. High and extremely high accuracy were common for woodpeckers and weak excavators, respectively (Fig. 9). BirdNET was >90% accurate for 13/19 secondary nesters (Fig. 10). No conclusions can be made on owls in general because 4/5 species had >66% false positive rates. Only the results of *Glaucidium passerinum* can be utilized, as its calls were identified correctly in 92-94% of samples.

Dendrocopos leucotos and *Picus canus* (Gray Woodpecker) remain listed as Least Concern, *P. tridactylus* as Near Threatened, and *Poecile montanus* (Willow Tit) was recently escalated to Vulnerable in Norway (Artsdatabanken, 2021). All have experienced alarming historical and current trends that warrant precautionary planning. These species joined other previously abundant birds like *Passer domesticus* (House Sparrow) and *Sturnus vulgaris* (European Starling) in a precipitous decline since the 1940s (Lampila et al., 2006). This paper cannot analyze the economic or cultural viability of the following recommendations, but, as a caveat, these should not be implemented if they would result in the immediate failure of a forestry operation or incentivize deforestation. I recommend implementing uneven-aged forestry in about half of the productive forests in the region. The return of structurally diverse forests with high-quality nesting trees and >21 m³ha⁻¹ deadwood may help the following birds reclaim areas where they have been extirpated and rebuild their population sizes (Hekkala et al., 2023, Kuuluvainen et al., 2021).

Willow Tit/Granmeis

Poecile montanus was the 4th most numerous bird in Finland before declining by 60% from the 1940s to the 1980s and by 15% from 1983 to the late 1990s (Väisänen, 2005). Two studies from Oulu in northern Finland studied *P. montanus* to determine the effects of clearcutting on this population; the first warned of the species becoming endangered in the future, while the second confirms this now-endangered species continues to struggle. Intensified clearcutting, fragmentation, and thinning are suggested to have reduced breeding pair density by 65% and threaten population persistence. Only clearcuts up to 30 years old were included, but the use of their proportion within 500m provides a useful estimate for landscape-level attributes. The proportion of clearcuts (and to a lesser extent, thinning) increased the nearest neighbor distance, but the number of snags reduced this distance (Kumpula et al., 2023). Winter home range size increased, and immigration would be hampered by forestry operations removing suitable snags and reducing food availability in winter (Lampila et al., 2006). My results found the opposite trend as *P. montanus* calls were twice as abundant in CC. I could not disprove any of BirdNET's identifications for this bird, suggesting that these findings reflected a true difference in activity. The population in southeastern Norway may have enough NN forest to use as a refuge while the CC stand regenerates, and there may be some food benefits or interspecific interactions in CC that remain undiscovered. Alternatively, the increase could be an artifact of a highly variable population growth rate (as in Finland) and represent a particularly good year in an otherwise sub-par environment (Lampila et al., 2006). Yet another possibility is that these birds prefer to forage in CC and return to NN for nesting, where they may remain quiet to avoid detection by predators.

Northern Goshawk/Hønsehauk and Eurasian Pygmy Owl/Spurveugle

Two raptors both great and small, Accipiter gentilis (Northern Goshawk) and Glaucidium *passerinum* (Eurasian Pygmy Owl), have correspondingly different lifestyles. The former is the largest raptor in the study, hunts a variety of birds and mammals, e.g., thrushes, crows, doves, squirrels, and hares, and is diurnal. The latter hunts tits, other songbirds, and rodents as the smallest owl in Europe. G. passerinum needs cavities to store food for the winter and raise its young, while A. gentilis never uses cavities. Yet these opposite ends of the spectrum were alike with stark differences between SiteTypes -9 and 7 times more activity, respectively, in NN. As expected, the heterogeneity of the natural disturbance regime supports more diverse niches than plantations (Kuuluvainen et al., 2021). Accuracy ratings were high for both, giving confidence in these results. Both raptors use older coniferous forests for their abundance and quality of nest sites. Large coniferous trees provide cover for the hawk's nest. The increased woodpecker activity improves the quantity and quality of cavities, thus enabling G. passerinum's unique life history to exist. As this owl does not commonly use manmade nest boxes, woodpeckers provide a much-needed service. Interestingly, the activity of G. passerinum increased at the same rate as Picoides tridactylus - sevenfold more in NN. Such a trend is telling yet not shocking considering how dependent the *pygmy* owl is on the second smallest woodpecker in the region to construct properly sized cavities (Svensson et al., 2021).

Three-toed Woodpecker/Tretåspett

As a keystone species, *Picoides tridactylus* impacts its ecosystem greater than its population would suggest. After a pair is finished excavating a cavity for themselves and raising their offspring, the cavity remains for a median of 10 years (Hardenbol et al., 2019). The yearly nest-making ritual opens nest sites and allows species like *G. passerinum* to inhabit forests

that would otherwise be unavailable to them. Dead and dying mature spruce and smaller deciduous trees are the home of *P. tridactylus* and its preferred prey, the larvae of the spruce bark beetle (*Ips typographus*). Depredating these beetles may dampen the frequency and severity effect of outbreaks in the area, benefiting both forest-dwellers and foresters with a less volatile supply of timber. The habitat requirements for and habitat modifications by this woodpecker also make it an indicator species for structural heterogeneity, habitat quality, and forest bird species richness.

Management requires solid targets, boundaries, and a sense of scale on the landscape to achieve its goals. As a bare minimum recommendation, a snag basal area of 0.9 m³ha⁻¹ is required for a 50-50 chance of Three-toed Woodpecker presence. Maintaining a volume of 18 m³ha⁻¹ of snags ≥ 10 cm DBH within a standard home range of 44-176 ha in spruce forests resulted in a 90% likelihood of finding *P. tridactylus* (Bütler et al., 2004). Standing deadwood passed the threshold at one Site in 5 Locations: 4/10 NN and only one CC. The ubiquitousness of industrial forestry has shrunk *P. tridactylus*'s range in Norway and shifted its Fennoscandian range from 50 years ago (Fig. 11). As mentioned above, this is the only woodpecker that is not listed as Least Concern on the Norwegian red list (Artsdatabanken, 2021). Serious support from the public and private sector is needed for this woodpecker, and the species that associate with it, to recover.



Fig. 11. Range reduction of three-toed woodpecker in Norway (top) and white-backed woodpecker in Europe (bottom) as seen in birding field guides of 1974 (left) and 2021 (right) (Peterson et al., 1974, Svensson et al., 2021). Right maps are cropped to match the scale of the left. Original illustrations from (Svensson et al., 2021).

White-backed Woodpecker/Hvitryggspett

The range of *Dendrocopos leucotos* used to span the lower half of Norway, where it lived in mixed and deciduous forests. Today, White-backed Woodpeckers have been extirpated from much of the East and now live in a thin coastal fringe. The startling loss of these woodpeckers in the last half-century in Fennoscandia has been noted in popular birding field guides in addition to scientific journals (Fig. 11). The Swedish population plummeted from breeding in 75% of the country's provinces before the 1950s to only 3 isolated patches and about 35 breeding pairs in the southern half of the country by 1995 (Carlson & Stenberg, 1995). The species is threatened with extinction in Sweden as the number continued to decline to only 12 breeding pairs (Rankka, 2021). In Finland, 95% of the population was lost in 30 years (Carlson, 2000).

Unsurprisingly, these declines track the conversion of nearly all productive forest and most deciduous forest in Fennoscandia to monoculture spruce/pine stands. A habitat analysis study in Western Norway, where this is the most common woodpecker, corroborates this. *D. leucotos* preferred deciduous forest with ample deadwood and no more than 40% of the surrounding 100 ha covered by plantation-style spruce (Gjerde et al., 2005). The authors predicted the conversion of native hardwood, birch, and pine forestland in Vestland to stop in the future. Unfortunately, the Norwegian government is considering further removal of pine and deciduous forests with non-native spruce. This perplexing idea is labeled as a "climate mitigation strategy," but it would destroy the mixed forests, release emissions that would take decades to reabsorb, and evict species from even more of their historical range (Kjønaas et al., 2021).

The plight of *D. leucotos* has resulted in species management plans in Sweden and Finland aiming to reverse the decline. This species has been promoted as an indicator of high-quality forest habitat as the woodpecker prefers about 20% of all stems to be snags and 75% to be deciduous trees. It is also pragmatic for forest management to use this charismatic, vocal bird as an umbrella species. Greater richness of bird species, red-listed birds, and red-listed species except beetles were found in conjunction with *D. leucotos* (Roberge et al., 2008). Norway could enhance forests for myriad taxa and bolster this woodpecker's recovery in the region by funding or incentivizing forest owners to improve their lands for this species instead of exacerbating the conversion to spruce monocultures. Without swift intervention, further fragmentation and local extinction of these declining species are expected (Carlson, 2000).

Conclusion

The specific effects of clearcutting on the species composition and activity of birds vary by species and functional group. Five of the seven woodpeckers preferred NN with the others having no preference. Most, but not all, weak excavators and secondary nesters were more likely to be detected in CC. Some non-cavity nester species greatly preferred one SiteType over another without an overall trend, but old-growth icons were certainly more common in NN. The scarcity of some woodpeckers and NN habitat features like cavities and deadwood may have cascading effects on the local and regional ecosystem.

The majority of bird species are just as active if not more so in CC, but many others experience steep declines. The homogeneity of CC being made almost entirely of thinner spruces under 80 years old can make it difficult for specialists and habitat engineers to persist. The three-toed and white-backed woodpeckers have suffered severe range reductions since the 1940s, with worsening trends in the last half-century. Although many secondary nesters are very active in CC, the lack of excavators may restrict their population size. Woodpeckers are vital for controlling wood-boring insects, creating nesting cavities, and supporting a variety of forest-dwelling birds. Managing for greater woodpecker diversity will create more and higher quality nesting sites for numerous other taxa, especially birds. In any stand, retaining aspen and ensuring its regeneration is the most effective way to improve nesting options for cavity-nesters, while oaks, birches, and other deciduous trees should be retained afterward. Doing so should improve conditions for both rare and common species.

A true mosaic landscape of intensive plantations, extensive forests, and primary forest preserves should increase resistance and resilience in the ecosystem and timber supply chain to outbreaks, severe weather, and changing abiotic conditions. Ecologically, this also allows the maximum number of species to thrive in boreal Fennoscandia.

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Appendix A: Natural History and Accuracy Ratings of Study Species

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Table A1. Natural history of all cavity nesters included in this study organized by nester type and average body length (BL). BL and preferences for *Strix uralensis* and *S. ulula* from Svensson et al. (2021). Reference from species account within Handbook of the Birds of the World Alive (del Hoyo et al., 2007).

Nester type	BL (cm)	Scientific	English	Norsk	Nesting preference/ Cavity in	Landscape preference	Reference
Excavator	43	Dryocopus martius	black woodpecker	svartspett	tall, usually living trees. Populus tremula (66%) Pinus sylvestris (32%)	any mature forest that is not extremely dark and closed	Winkler and Christie 2002
	33	Picus viridis	green woodpecker	grønnspett	unbroken trees. Populus tremula (88%)	wide variety of semi- open habitats near mature deciduous or coniferous trees	Winkler and Christie 2015
*	29.5	Picus canus	grey woodpecker	gråspett	deciduous trees of multiple species. Populus tremula (91%)	wide variety of habitats with deciduous trees or open coniferous forest	Winkler and Christie 2015
	26.5	Dendrocopos leucotos	white-backed woodpecker	hvitryggspe tt	trees, branches, stumps. Betula sp. (45%) Populus tremula (36%)	old growth and overmature deciduous and mixed forests with ample dead wood.	Winkler and Christie 2002
,	24.5	Dendrocopos major	great spotted woodpecker	flaggspett	trees, branches, stumps. Populus tremula (78%) Betula sp. (12%) generalist	any woodland or forest	Winkler et al. 2015
	22.75	Picioides tridactlyus	three-toed woodpecker	tretåspett	trees. Picea abies (69%) Populus tremula (31%)	mature coniferous spruce forest, especially where local insect populations are booming	Winkler et al. 1995
	15.25	Dendrocopos minor	lesser spotted woodpecker	dvergspett	trees, branches, stumps. Populus tremula (40%) Betula sp. (34%) Alnus sp. (26%)	deciduous open woodland with thin snags near water	Winkler and Christie 2002

Weak excavator	13.25	Sitta europaea	Eurasian nuthatch	spettmeis	mature or old trees	mixed/deciduous forest	Harrap 2015
	12.5	Poecile montanus	willow tit	granmeis	rotting trees or stumps <3m	coniferous or wet areas	Gosler et al. 2013
	11.25	Lophophanes cristatus	crested tit	toppmeis	dead/decaying branches, trees, stumps, nestboxes	spruce and pine forests	Gosler & Clement 2007
Secondary	66	Bubo bubo	eagle-owl	hubro	*rarely in a tree hole, usually on cliff edges, crevices, and taiga ground*	secluded rocky country, taiga, forests, woodlands, farmlands with rocky areas	Holt et al. 2013
Secondary	54.5	Strix uralensis	Ural owl	slagugle	"chimney tree" or raptor nests†	old coniferous forest with mires, often next to water, clearings, and cultural landscapes [†]	NA
Secondary	44	Bucephala clangula	goldeneye	kvinand	mature trees (aspen, oak, spruce)	shallow water, open confierous forest, marshes with solitary trees near the edge	Johnsgard 1978, Flint et al. 1984, del Hoyo et al. 1992, Kear 2005
Secondary	40	Strix aluco	tawny owl	kattugle	trees, cliffs, buildings and steep river banks; old nests of other animals	any forest, cultural landscapes, urban	Holt et al. 1999
Secondary	39	Surnia ulula	Northern hawk owl	haukeugle	"chimney tree" or regular cavities in trees, old twig nests†	mountain birch- coniferous forest zone, esp. near mires, meadows, and clearcuts†	NA
Secondary	32	Corvus monedula	western jackdaw	kaie	trees, chimneys, rock formations, etc. *sometimes constructed openly in bushes*	any open country, prefers scattered trees	Madge & de Juana 2014

Secondary	24.5	Aegeolius funereus	boreal owl	perleugle	esp. svartspett cavities in trees or free-standing nest†	coniferous forest, esp. dense and old growth, some agricultural land	Korpimäki & Hakkarainen 2012
Secondary	20.5	Sturnus vulgaris	sarling	stær	tree, cliff, manmade structure, nestboxes	various incl. open country, woodland, scrub, suburban, urban	Craig & Feare 2015
Secondary	17	Jynx torquilla	Eurasian wryneck	vendehals	hardwood trees, nest boxes	open woodlands, orchards, unimproved meadows	Winkler et al. 2015
Secondary	17	Glaucidium passerinum	Eurasian pygmy owl	spurveugle	esp. flaggspett and tretåspett cavities in deciduous trees, nest boxes†	open coniferous/mixed forest with tall interior	Holt et al. 1999
Secondary	15	Passer domesticus	house sparrow	gråspurv	manmade esp. buildings, cliffs, trees	any level of human habitation	Summers- Smith et al. 2015
Secondary	14.25	Muscicapa striata	spotted flycatcher	gråfluesnap per	trees, branches, stumps	well-spaced woodland, bushes with clearings	Taylor 2015
Secondary	14.25	Parus major	great tit	kjøttmeis	any tree, manmade esp. nest boxes	various: functionally any group of trees or shrubs	Gosler et al. 2013
Secondary	13.8	Phoenicurus phoenicurus	common redstart	rødstjert	trees, old stumps, stone walls, nest boxes	any open forest or woodland; mountain birch and pinelands in Northern Europe	Collar and Christie 2015
Secondary	13.25	Certhia familiaris	treecreeper	trekryper	*loose bark or crevice* <16 m in older trees	older spruce stands	Harrap 2015
Secondary	13.25	Erithacus rubecula	European robin	rødstrupe	always in a recess in various sites incl. tree cavity, tree roots, nest boxes	various incl. forest- open gradient, edges	Collar 2015
Secondary	13.25	Passer montanus	Eurasian tree sparrow	pilfink	tree, cliff, earth bank, manmade	cultivated lands; sometimes light	Summers- Smith 2016

						woodland, built-up areas	
Secondary	12.5	Ficedula hypoleuca	European pied flycatcher	svarthvit fluesnapper	trees, nest boxes	mixed/deciduous open, sunny, mature woodlands	Taylor & Christie 2015
Secondary	12.25	Poecile palustris	marsh tit	løvmeis	deciduous trees, stumps, upturned root balls	mature deciduous woodland/forest	Gosler et al. 2013
Secondary	11	Cyanistes caeruleus	blue tit	blåmeis	(and clefts in) trees, manmade esp. nest boxes	deciduous woodland, parks, urban; avoids dense conifer stands	Gosler et al. 2013
Secondary	10.75	Periparus ater	coal tit	svartmeis	trees, old stumps	conifer forest, plantations, (sub)urban	Gosler & Clement 2007
Secondary	9.75	Troglodytes troglodytes	winter/Eurasian/ Northern wren	gjerdesmett	*free-standing in dense vegetation* or cavity/crevice in various sites incl. manmade	various from woodland to urban to sparse scrubland	Kroodsma et al. 2015

Table A2. Validation of BirdNET's accuracy for 34 species of cavity nesters and old-growth icons (*). Three old-growth icons (*Poecile cinctus* n = 27, *Phylloscopus trochiloides* n = 5, & *Tarsiger cyanurus* n = 109), from (Virkkala & Rajasärkkä, 2006) were removed as they were most likely similar calls from other, better documented species in southeastern Norway. T = true identification, F = false-positive, U = unknown that could not be confirmed nor denied, and n = validation samples for that species. Accuracy is calculated as (T + U)/n.

Nester type	Scientific name	Common name	Accuracy	Т	F	U	n	Authority
Excavator	♣ Dryocopus martius	Black Woodpecker	0.96	96	3	1	100	(Linnaeus, 1758)
Excavator	Picus viridis	Eurasian Green Woodpecker	0.417	15	18	3	36	Linnaeus, 1758
Excavator	Picus canus	Gray-headed Woodpecker	0.84	84	13	3	100	J. F. Gmelin, 1788
Excavator	Dendrocopos leucotos	White-backed Woodpecker	0.378	14	6	17	37	(Bechstein, 1802)
Excavator	≉ Dendrocopos major	Great Spotted Woodpecker	0.99	99	1	0	100	(Linnaeus, 1758)
Excavator	♣ Picoides tridactylus	Eurasian Three-toed Woodpecker	0.48	48	48	4	100	(Linnaeus, 1758)
Excavator	Dryobates minor	Lesser Spotted Woodpecker	0.183	15	65	2	82	(Linnaeus, 1758)
Weak excavator	Sitta europaea	Eurasian Nuthatch	0.96	96	3	1	100	Linnaeus, 1758
Weak excavator	Poecile montanus	Willow Tit	1	100	0	0	100	(Conrad von Baldenstein, 1827)
Weak excavator	♣ Lophophanes cristatus	Crested Tit	1	100	0	0	100	(Linnaeus, 1758)
Secondary	Bubo bubo	Eurasian Eagle-Owl	0.061	4	59	3	66	(Linnaeus, 1758)
Secondary	Strix uralensis	Ural Owl	0.07	7	91	2	100	Pallas, 1771
Secondary	Bucephala clangula	Common Goldeneye	0.333	1	1	1	3	(Linnaeus, 1758)
Secondary	Strix aluco	Tawny Owl	0.32	32	62	6	100	Linnaeus, 1758
Secondary	Aegolius funereus	Boreal Owl	0.31	31	68	1	100	(Linnaeus, 1758)
Secondary	Glaucidium passerinum	Eurasian Pygmy-Owl	0.93	93	6	1	100	(Linnaeus, 1758)
Secondary	Passer domesticus	House Sparrow	1	1	0	0	1	(Linnaeus, 1758)
Secondary	Muscicapa striata	Spotted Flycatcher	0.99	99	1	0	100	(Pallas, 1764)
Secondary	Parus major	Great Tit	1	100	0	0	100	Linnaeus, 1758
Secondary	♣ Phoenicurus phoenicurus	Common Redstart	1	100	0	0	100	(Linnaeus, 1758)

Secondary	≉ Certhia familiaris	Eurasian Treecreeper	1	100	0	0	100	Linnaeus, 1758
Secondary	Erithacus rubecula	European Robin	0.97	97	3	0	100	(Linnaeus, 1758)
Secondary	Passer montanus	Eurasian Tree Sparrow	1	32	0	0	32	(Linnaeus, 1758)
Secondary	Ficedula hypoleuca	European Pied Flycatcher	0.94	94	4	2	100	(Pallas, 1764)
Secondary	Poecile palustris	Marsh Tit	0.94	94	6	0	100	(Linnaeus, 1758)
Secondary	≉ Ficedula parva	Red-breasted Flycatcher	0.68	68	27	5	100	(Bechstein, 1792)
Secondary	Cyanistes caeruleus	Eurasian Blue Tit	0.98	98	2	0	100	(Linnaeus, 1758)
Secondary	Periparus ater	Coal Tit	0.99	99	0	1	100	(Linnaeus, 1758)
Secondary	Troglodytes troglodytes	Eurasian Wren	0.98	98	1	1	100	(Linnaeus, 1758)
non-cavity	≉ Tetrao urogallus	Western Capercaillie	0.14	14	84	2	100	Linnaeus, 1758
non-cavity	<i>▲</i> Accipiter gentilis	Northern Goshawk	0.8	80	17	3	100	(Linnaeus, 1758)
non-cavity	♣ Perisoreus infaustus	Siberian Jay	1	12	0	0	12	(Linnaeus, 1758)
non-cavity	≉ Turdus viscivorus	Mistle Thrush	0.94	94	6	0	100	Linnaeus, 1758
non-cavity	♣ Pinicola enucleator	Pine Grosbeak	0.951	58	2	1	61	(Linnaeus, 1758)

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