Using passive acoustic monitoring to compare bird communities across restoration treatments in Swedish boreal forests

Elisa Michiels

Master Thesis • 60 credits
Swedish University of Agricultural Sciences, SLU
Department of Wildlife, Fish, and Environmental Studies
Management of Fish and Wildlife Populations – Master’s programme
Examensarbete / SLU, Institutionen för vilt, fisk och miljö
2025:26
Umeå, 2025

Image: Nele Otto

Using passive acoustic monitoring to compare bird communities across restoration treatments in Swedish boreal forests

Elisa Michiels

Supervisor:	**Wiebke Neumann Sivertsson, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies**
Assistant supervisor:	Anne-Maarit Hekkala, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies
Examiner:	Tim Hofmeester, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies

Credits:	60 credits
Level:	Second cycle, A2E
Course title:	Master's thesis in Biology, A2E – Wildlife, Fish, and Environmental Studies
Course code:	EX0970
Programme/education:	Management of Fish and Wildlife Populations – Master's programme
Course coordinating dept:	Department of Wildlife, Fish, and Environmental Studies
Place of publication:	Umeå, Sweden
Year of publication:	2025
Title of series:	Examensarbete / SLU, Institutionen för vilt, fisk och miljö
Part number:	2025:26

Keywords:	Forest restoration, bird community, species richness, forest structure, passive acoustic monitoring, treatment, functional groups

Swedish University of Agricultural Sciences
Faculty of forest sciences
Department of Wildlife, Fish, and Environmental Studies

Abstract

Ecosystem degradation has driven global restoration efforts aimed at recovering biodiversity and ecosystem services. Intensive forestry practices in Sweden's boreal forests have altered forest structure, thereby impacting biodiversity. This study assesses whether forest restoration enhances habitat complexity and supports bird diversity, using birds as indicators of ecological health. Passive acoustic monitoring (PAM) was employed to record bird vocalizations across 30 forest stands in two of Sveaskog's Ecoparks, one in northern (Käringberget) and one in southern (Hornsö) Sweden. Each Ecopark includes forest stands representing three treatment types: target, restored and unrestored. Structural habitat variables such as deadwood volume, basal area, and understory cover were measured to evaluate habitat complexity. Results showed that restoration increased structural similarity between target and restored stands, particularly in Hornsö, while unrestored stands remained distinct. Bird species richness and community composition showed limited overall responses, though certain functional traits and indicator species reflected treatment differences. Structural variation within stands and subtle bird responses suggest that restoration is a gradual process, with key features like deadwood volume and conifer basal area playing important roles in shaping bird assemblages. This study highlights the value of combining structural metrics and PAM to evaluate restoration outcomes for forest and bird biodiversity.

Keywords: Forest restoration, bird community, species richness, forest structure, passive acoustic monitoring, treatment, functional groups

Table of contents

List of tables

List of figures

Abbreviations

Abbreviation	Description
GLM	Generalized linear model
ISA	Indicator species analysis
NMDS	Non-metric multidimensional scaling
PAM	Passive acoustic monitoring

1. Introduction

Biodiversity loss has reached a critically dangerous stage, surpassing even climate change in its impact, leaving the planet unable to recover naturally without intervention (Steffen et al., 2015). The loss of species has reached alarming levels, with an estimated 1 milion out of the 8.7 million species on earth currently at risk of extinction (IPBES, 2019). Ecosystem degradation has become a known issue across various biomes, promoting global efforts to restore biodiversity and ecosystem services (Foley et al., 2005; CBD, 2010). Ecological restoration is defined as the process of supporting the recovery of ecosystems that have been degraded, damaged or destroyed allowing for revitalization of natural habitats (Society for Ecological Restoration, 2004). This emphasizes the importance of not just retruning ecosystems to a previous state, but also implementing active management strategies to achieve this goal (Hobbs et al., 2009; Jackson & Hobbs, 2009). Historicaly and recently human exploitation has led to alterations in forest dynamics, tree age distributions and changes in species compositions (Wallenius et al., 2010; Siitonen, 2001; Brumelis et al., 2011). Measures to restore forest functions often include improving hydrology, modifying forest structure, and ensuring that restoration actions are compatible with the needs of specific species (Komonen & Kouki, 2008; Olsson et al., 2011). Given the complex interplay between species requirements and habitat dynamics, successful restoration must consider both the current ecological state and the ecosystem's potential for recovery (Wilson et al., 2011; Kouki et al., 2012).

Restoration ecology is a relatively young science and with biodiversity in decline, alternative forest management strategies are becoming increasingly important. In managed forest landscapes, biodiversity values can suffer due to intensive wood production practices (Rompré et al., 2010). Balancing biodiversity conservation with ongoing economic development present a significant challenge for human society. Although sustainable development relies heavily on healthy ecosystems, economic growth and biodiversity conservation, which are often perceived to be incompatible (Lubchenco, 1998). The forestry practices in Sweden's boreal forests have significantly impacted both the landscape and biodiversity. The loss of old-growth forests and natural habitats with long-term ecological continuity has led to a decline in high conservation value area, severely threatening species diversity (Hämäläinen et al., 2018; Swedish forestry agency [SFA], 2022). In this context, green infrastructures (GI), a strategically planned network of natural and semi-natural areas, is essential for improving ecological functions at the landscape-level and providing key ecosystem services. To create functional GI, it is necessary to expand and connect the remaining biological values in the landscape. This includes linking core natural areas and regions of high conservation value through green corridors, enabling the dispersal of threatened species and strengthening ecological resilience (Karlsson et al., 2024). Within this broader strategy, ecoparks provide a promising solution, for integrating nature conservation and human recreation within managed forest landscapes. Their goal is to safeguard biological diversity by prioritizing ecological values over the economic ones. Sveaskog, the largest state-owned forest owner in Sweden, has established 37 ecoparks with the goal of preserving high nature values and improving ecological conditions to support environmental goals (Sveaskog, n.d.).

Birds are widely recognized as important indicators of habitat quality and ecological health. They are used as environmental indicators due to their sensitivity to changes in forest structrure and landscape composition (Gregory & Van Strien, 2010). By monitoring bird populations, we can gain insights into how restoration measures influence biodiversity. Numerous studies have shown that the abundance and species richness often mirror broader biodiversity trends in different habitat types, including urban, agricultural and forested areas (e.g., in temperate ecosystems, tropical ecosystems, grassland habitats, croplands, urban parks, etc.) (Eglington et al., 2012; Sattler et al., 2013; Valerio et al., 2016). A central objective of ecological restoration is to reinitiate natural processes that promote structurally diverse forest ecosystems (Jackson & Hobbs, 2009; Halme et al., 2013). Yet, intensive forest management, particularly when driven by timber production, has often led to habitat simplification, reduicing the presence of key ecological features essential for many species (Van Der Plas et al., 2016). This simplification frequently begins with the loss of deadwood and mature, large-diameter deciduous trees, both of which provide crucial resources for forest organisms (Kuuluvainen, 2002; Wesolowski, 2005). In such environments, bird species may experience reduced foraging opportunities due to lower invertebrate availability, increased exposure to predation, lack of diverse nesting, feeding and shelter opportunities (Spies et al., 2006; Storch et al., 2018; Paillet et al., 2015; Bujoczek et al., 2021; Piazzi et al., 2020). Furthermore, the composition of bird communities can shift depending on the amount and quality of available habitat, often favoring generalists over specialists in fragmented or disturbed landscapes (Uezu & Metzger, 2011). At the local scale, species abundance is closely linked to forest structural complexity (Balestrieri et al., 2015; Czeszczewik et al., 2014), while landscape-level habitat configuration influences species distribution and overall diversity (Basile et al., 2016; Komonen & Kouki, 2018).

Passive acoustic monitoring (PAM) has become an increasingly valuable tool for long-term and cost-effective biodiversity monitoring through unattended sound recording (Sugai et al., 2018). Many animals produce acoustic signals, vocalisation that carry information about their presence, behaviors, and interactions in space and time (Kershenbaum et al., 2014). PAM is noninvasive, autonomous method that offers a broad detection range. Compared to traditional survey methods, PAM provides the advantage of continuous monitoring with minimal human effort. Species detections from PAM can support a wide range of ecological applications, from estimating species occupancy to assessing biodiversity (Gibb et al., 2018). Soundscapes recorded through PAM, can reveal ecosystem changes caused by both sudden or long-term disturbances. They capture information on biotic and abitotic aspects of ecosystems, and they also allow for monitoring post-distrubance recovery. PAM can capture succession and community assembly dynamics, aiding in the evaluation of restoration progress (Ross et al., 2023). Bioacoustics, the scientific study of sound production, transmission, and reception in animals, is central to PAM (Sueur et al., 2014). This approach yields valuable insights into bird activity, which is often linked to habitat structure and can serve as an indicator of habitat quality (Shaw et al., 2021). A richer and more complex sound environment typically reflects greater biodiversity (Dröge et al., 2020). Recent advances in automated sound recording and analysis offer great potential for fast, large-scale biodiversity monitoring. Research can build on this by investigating how natural soundscapes change over time, how multiple stressors interact to influence animal acoustic activity, and how long it takes ecosystems to reflect the effects of disturbance or recovery (Burivalova et al., 2019; Laiolo, 2010).

1.1 Research objectives

Restoration of degraded habitats is often employed as a tool for ecological compensation, but is there an actual impact on bird biodiversity? Restoration efforts are believed to enhance habitat complexity and the availability of critical resources (Halme et al., 2013). Yet, within the context of restoration ecology, we still lack sufficient knowledge whether target ecosystems (i.e. high species composition and functional traits, different habitat features, self-sustainability, resistance and recovery, functional connectivity, etc.) are truly as beneficial for bird biodiversity as we assume. The primary purpose of this research is to answer the following research question:

How do bird community structure differ among target, restored and unrestored ecosystem forest stands with varying levels of broadleaves and deadwood within managed forest landscapes?

The aim is to assess whether more structural heterogeneity and complexity influence bird occurrence. By determining how different restoration activities alter forest structures and subsequently bird biodiversity. Additionally, the research will identify which structural features are most beneficial for bird habitats. To achieve this objective, this research addresses the following research questions:

I. How does structural complexity vary across forest restoration treatments within ecoparks? Specifically, do structural measurements differ between treatments (target, restored and unrestored stands)? Is there variation within a stand based on plot comparision, and is restoration applied uniformly across the entire stand?

   Hypothesis: Target stands are anticipated to display structural characteristics that closely reflect natural forest dynamics. Restored stands are expected to resemble target stands, exhibiting greater structural complexity, including higher deadwood volumes and higher presence of broadleaved trees, compared to unresrored stands. These restoration efforts are expected to be consistent across all stands and treatment types.

II. How does the bird species richness and community composition vary across treatment (target, restored and unrestored)? Can functional traits, such as nesting and foraging strategies provide further insights into these patterns? Furthermore, how does forest structural complexity, including factors like tree species composition, deadwood and basal area, influence these bird assemblages, and which structural features are most strongly correlated with bird diversity and habitat use?

Hypothesis: Bird species richness is expected to be higher in target and restored stands compared to unrestored stands, as restoration efforts aim to enhance habitat conditions. Community composition is also anticipated to differ among treatments, with target and restored stands supporting more specialized or diverse species assemblages. These differences may be evident in both species identities and distribution of functional traits, with structurally complex habitats favoring certain ecological strategies. Moreover, increased structural complexity will positively correlate with higher bird assembalges.

III. Can indicator species be distinguished within each area, reflecting the biotic or abiotic conditions of the environment? Do these species provide evidence of environmental changes, serve as predictors of broader species diversity, or indicate the composition of taxa and communities in a given area?

Hypothesis: Certain species will be specific to particular treatment, highlighting key environmental features. Since restoration practices are expected to influence bird species, some species may serve as indicators of these habitat changes.

IV. Are the responses of bird assemblages to restoration actions similar across regions of Sweden?

Hypothesis: The responses of bird assemblages to restoration actions will show similarities across different regions of Sweden, indicating that common structural features resulting from restoration efforts consistently benefits bird populations. However, bird assemblages in the southern regions will exhibit higher species richness and abundance due to a greater presence of broadleaf tree species compared to northern regions.

2. Materials & Methods

2.1 Study areas & sites

This study is part of a long-term initiative, the Effekt 20 project, aimed at assessing landscape-scale management's impacts on ecological diversity over an extended period of 50 years. Within this framework, our research focuses on two Ecoparks spread over two major ecozones in Sweden, the hemiboreal and the boreal zone. The Ecoparks are managed following Sveaskog's environmental policy, which requires that 20% of productive forest land in each region is reserved for nature conservation and protection. This commitment to ecological integrity is operationalized through Sveaskog's division of forest holdings into ecological landscapes, classified into four forest management categories commonly used across Sweden to balance timber production and conservation goals. In most protected areas, known as NO-stands, no forestry activities are permitted, allowing these untouched forests to evolve naturally. NS-stands maintain a conservation focus with minimal forestry activity, such as selective logging. PG-stands, primarily used for production, incorporate additional conservation measures like buffer zones and key habitat protection to support both ecological sustainability and resource use. PF-stands, are primarily managed for timber production. In this study, all selected stands fall under the NO-stand management category (Sveaskog, 2005; Sveaskog, 2008).

Established in 2004, Hornsö Ecopark spans 9 200 hectares and is located in Högsby and Nybro municipalities in Kalmar County (56.986°N, 16.100°E). Hornsö is particularly valued for its diversity of wood-inhabiting insects, hosting northern europe's richest community, including around 230 red-listed species. This area is ecologically diverse, featuring an array of forest types, such as ancient pine, broadleaf, and swamp forests, all managed with specific conservation targets. Restoration within Hornsö prioritizes noble broadleaf forests, targeting oak, beech, ash, lime and maple, which support rare and high-value habitats. Restoration efforts focus on increasing biodiversity, with nearly 1 900 hectares of forests which is about 35% of the productive forest area. The efforts include restoring historical fire regimes, selective thinning to increase broadleaf tree density, and wetland restoration to enhance habitat connectivity (Sveaskog, 2008).

Käringberget Ecopark, inaugurated in 2005, was established within the municipality of Frederika, Västerbotten County (64.120°N, 18.664°E). Covering approximately 14 000 hectares, of which 10 900 hectares are productive forest, the ecopark hosts a dynamic mix of habitats, including ancient pine forests, old-growth spruce forests, deciduous woodlands, and forested wetlands. Large aspen clones and old birch forests further enrich its ecological diversity. The landscape is primarily forested (78% of the area), punctuated by 1 766 hectares of mire, 834 hectares of water bodies, and smaller areas of mountainous terrain and pasture. Key conservation efforts include the preservation of old-growth pine and spruce forests, abundant deadwood and the reintroduction of controlled burns. Selective cutting is used to remove less desired species and promote aspen and birch growth. In unrestored areas, buffer zones protect streams and sensitive sites, and selective logging methods preserve valuable trees to support biodiversity (Sveaskog, 2005).

Figure 1: Map of Sweden with the location of Northern (Käringberget) and southern (Hornsö) study areas.

2.2 Sampling design

In total, 15 stands were selected from each ecopark, resulting in 30 stands distributed across the two ecoparks. Each ecopark included three categories of stands: five target stands, five restored stands, and five unrestored stands. The target stands represent the desired post-restoration conditions that the ecoparks aim to achieve. The restored stands have undergone restoration measures and are expected to develop toward conditions similar to the target stands over time, while the unrestored stands serve as control areas, reflecting conditions prior to any restoration efforts. Each stand included five plots for structural measurements, with one plot designated for acoustic monitoring. This setup led to a total structural measurement effort across 75 plots, with 15 acoustic boxes placed throughout each park. The acoustic boxes were placed in the center of a given forest stand. To generate the five random plots, a 50 meter buffer was created to prevent overlap.

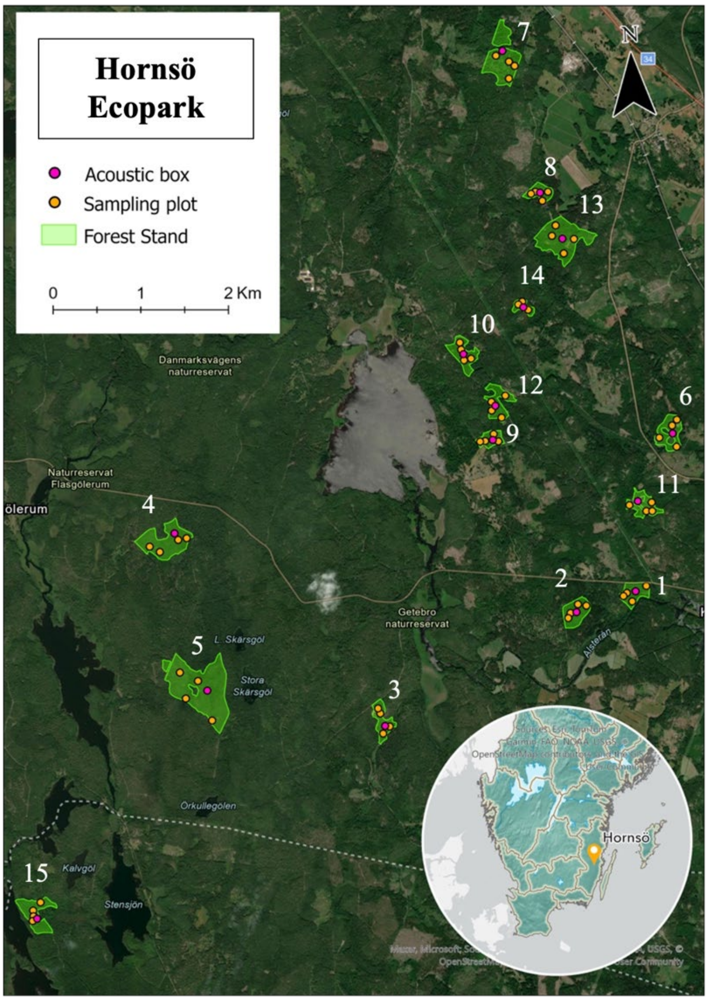


Figure 2: Sampling design in Hornsö Ecopark (2024), showing the distribution of random sampling plots (orange dots) and the placement of the acoustic box (pink dot). Forest stand boundaries and locations are shown in green. Treatment classifications include: target stands - 2, 7, 8, 12, 15; restored stand - 1, 9, 10, 11, 13; unrestored stand - 3, 4, 5, 6, 14. The sampling design for Käringberget design is provided in Appendix 1.

2.3 Field measurements – Forest survey

Field measurements in this study focused on capturing the structural characteristics of forest stands to quantify habitat complexity. Measured structural attributes included deadwood volume (m^3/ha), basal area (m^2/ha) and understory cover (m^2/ha) composition.

Deadwood was assessed in circular plots with a 10 meter radius. Within these plots, lying deadwood (logs) and standing deadwood (snags and high stumps) with a minimum diameter of 10 centimeter and a length or height of at least 1,3 meters were included. For lying deadwood, length and diameter were recorded, while for snags, diameter at breast height (DBH) and total height were measured. Trees partially lying and partilly standing, were considered lying if they formed an angle of less than 45° with the ground. A decay classification was assigned to capture various stages of decomposition. For logs, a modified version of Söderström's classification was used:

- DC1: Wood is hard, with intact or mostly intact bark.
- DC2: Wood remains hard but has a softened surface, with less than 50% bark remaining.
- DC3: Wood is soft with crevices, lacking bark and may show surface irregularities.
- DC4: Wood is very soft, often with an indistinct shape and outline.

For snags, decay classes (1 to 7) were assigned based on visual stages illustration in Figure 3 (Thomas et al., 1979).

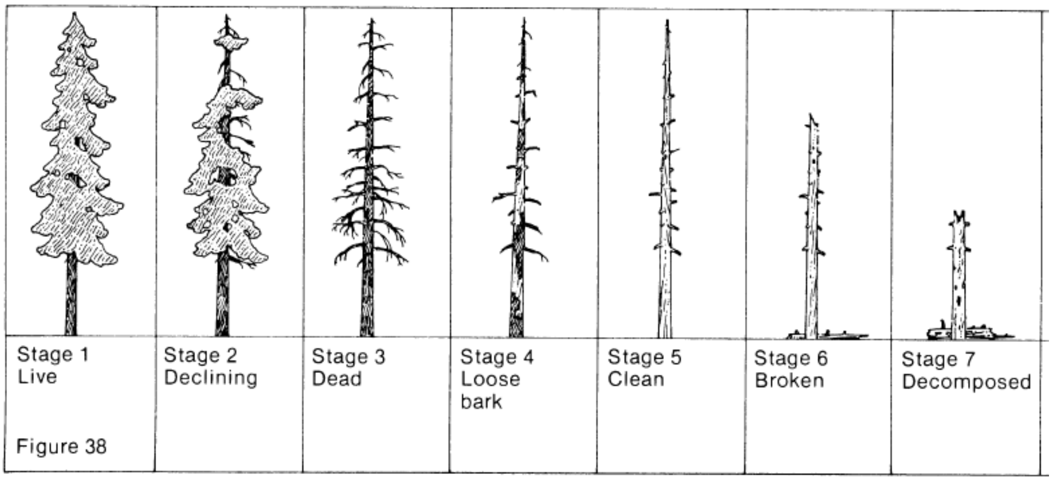


Figure 3: Standing deadwood, decay classification.

Alongside the visual assessment, a knife method was used to classify deadwood based on the depth a knife could penetrate (Table 1). Combining this method with visual inspection ensured a more consistent and accurate estimate of wood decay and woody debris mass.

Table 1: Description of the knife method, which sort deadwood items into different decay classes.

Decay class	Description
1	Recently dead tree, wood still hard, knife blade penetrates a few milimeters into the wood.
2	Weakly decayed wood of outer layers of stem has started to soften, wood still fairly hard, knife blade penetrates 1-2 cm into the wood.
3	Medium decayed wood of outer layers of stem fairly soft, core still hard, knife blade penetrates 2-5 cm into the wood.

4	Very decayed wood soft throughout the log, no hard core, knife blade penetrates all the way through the wood.

Deadwood data, including both logs and snags, were calculated at the plot and stand levels and expressed in volume per hectares. Plot-level calculations enabled comparisons within stands, while stand-level values allowed for comparisons between stands. Deadwood volume for logs was calculated using the formula for truncated cones, while the volumes for snags were calculated using Näslund (1947) taper equation, with species-specific formulas applied for conifers and broadleaves (Appendix 2). Conifers included pine and spruce, while for all broadleaved trees the volume was calculating using the birch formula. This due to the lack of species-specific formulas for many Swedish broadleaf species (Fridman & Walheim, 2000). Deadwood volume for broken trees (e.g., snags decay classification 6 and 7) was not calculated due to their limited occurrence in the dataset and to simplify the analysis. In addition to deadwood, smaller trees less than 1,3 meters in height and 4,5 centimeter in diameter were counted by species within a 1,78 meter radius subplot to capture understory tree density and composition. Aditionally, basal area was estimated for living trees using a relascope with a one-centimeter setting. Trees visible through the relascope were identified and counted by species to estimate species-specific basal area, expressed per hectare.

2.4 Bird sampling – Acoustic survey

The acoustic survey was conducted following a carefully planned setup. Data collection was carried out for a total duration of four weeks, starting in mid-April or May (Hornsö: 13 Apr – 13 May; Käringberget: 21 May – 23 June), depending on the ecopark's location. The variation in starting dates reflects differences in the timing of spring arrival, which occurs earlier in the south than in the north. This approach ensured that surveys aligned with local phenological conditions. In each stand, only one acoustic box was installed. However, one box from Käringberget did not provide usable data due to water damage, resulting in no data from that stand.

Recordings were taken continuously over a 24-hour cycle, with one-minute recordings captured every ten minutes. From this large dataset, a subset of recordings was selected using a standardized protocol to ensure consistent and representative sampling of bird vocal activity. Each full hour consisted of six one-minute recordings (6 recordings x 10 minutes = 60 minutes = 1 hour). For analysis, one of these six recordings was randomly selected per hour, resulting in 24 one-minute recordings per day. To increase coverage during the peak of bird vocal activity, this daily sample was complemented by additional two recordings taken during the early morning hours, with a focus on the sunrise period. For Hornsö, this intensified sampling window spanned from 4:00 to 10:00, while for Käringberget, it extended from 1:00 to 10:00 due to earlier sunrise times in the north. The selection of which minute to extract within each hourly window followed a randomization protocol implemented in R.

To analyze bird presence in the recordings, species were identified based on their acoustic vocalizations. Each bird species has distinct vocal signatures that can vary depending on context, such as territorial songs, alarm calls, or contact calls. By recognizing and distinguishing these different vocal patterns, it was possible to determine which species were present in the study area. The analysis was performed using the program Kaleidoscope Pro (www.wildifeacoustics.com). Recordings were analyzed in the non-bat analysis mode to ensure the parameters were suited to capturing bird vocalizations. The software scanned for signals within the frequency range of 250 Hz to 10 kHz. It detected continuous signals between 0.1 to 7.5 seconds and separated distinct calls using a 0.35 second silence threshold. Once signals were detected, an unsupervised clustering algorithm grouped similar vocalizations into clusters based on shared characteristics such as frequency, duration and structure. Following the recommendation of Kaleidoscope Pro software, I listened to the first ten recordings of each cluster, followed by one randomly selected recording every 40 entries, and finished with the last ten recordings of the cluster. This approach ensured that variation within clusters was captured. To identify the calls, I relied on my own experience and knowledge, supplemented by reference books, online resources such as Xeno-Canto, and identification apps like Merline Bird ID and BirdNET. Additional guidance was provided by a colleague with expertise in bird vocalizations. When a vocalization was confidently identified to species level, it was saved in a set of control files for future references. This helped streamline the process by allowing quick comparisons with new, unlabelled calls. The full bird species list per acoustic box is provided in Appendix 3.

For this analysis, species not typically associated with forest habitats, were excluded or retained based on information from BirdLife International (2024), Mikusinski et al. (2018), and Versluijs et al. (2020) (Appendix 4).

2.5 Statistical Analysis

2.5.1 Forest structural complexity

To test for differences among treatments within each ecopark for the various structural features, the non-parametric Kruskal-Wallis test was applied, followed by Post-hoc Dunn's test for pairwise comparisons. To compare the overall structural composition among the treatments, a two-dimensional non-metric multidimensional scaling (NMDS, function "metaMDS"), based on Bray-Curtis dissimilarities was perfomed. The "envfit" function was applied to fit environmental variables onto the NMDS ordination to calculate the centroids and ellipses representing group-level variation. Differences among treatments were tested for statistical significance using PERMANOVA (Permutation-based analysis of variance) (Anderson, 2001) using the "adonis" function from the package "vegan" in R (Oksanen et al., 2022). Further, to assess the homogeneity of groups dispersions (i.e., multivariate variances), the "betadisper" function (Anderson, 2005; Anderson et al., 2006) from the package “vegan” was used. This analysis was conducted at both plot and stand levels to capture variation within and among stands.

2.5.2 Bird species richness and composition

Differences in species richness across treatment were analyzed using an ONE-WAY ANOVA followed by a TukeyHSD (Tukey’s Honest Significant Difference) for pairwise anaylsis in case of significance. Similarly to the structural data, bird species composition differences between treatments were visualized using NMDS and tested with PERMANOVA (Anderson, 2001). The “envfit” function was applied to fit bird community variables onto the NMDS ordination to calculate centroids and ellipses representing variation in community composition. Further, to assess the homogeneity of groups dispersions (i.e., multivariate vairances), the “betadisper” function was used (Anderson, 2005; Anderson et al., 2006). Species richness was also assessed within defined functional groups, representing birds that share common ecological traits such as feeding strategy, nesting behavior, or habitat preference (Appendix 5). To test for differences in species richness between functional groups, the Kruskal-Wallis test was applied. When significant differences were found, pairwise comparisons were conducted using the Wilcoxon rank-sum test. Additionally, group mean comparisons were conducted to further examine differences between functional groups. To assess differences in species richness within a specific functional group (e.g., cavity nesters) between the treatments, the Kruskal-Wallis test was again used, followed by Dunn’s post-hoc test for pairwise comparisons.

2.5.3 Indicator species analysis

Indicator species analysis was performed using the “multipatt” function from the “indecspecies” package (De Cáceres & Legendre, 2009). This analysis compares the relationship between species occurrence and sites, in this case, “sites” are the three different treatments. Species indicator value is derived from two indices: the A-index, which represent “specificity”, (i.e., the degree to which a species is restricted to a particular group), and the B-index, which reflects “fidelity,” (i.e., the frequency of the species within that group). The indicator species index combines the A and B indice, identifying species that are both frequent and exclusive to a specific treatment.

2.5.4 Relationship between structural complexity and species richness

To test which structural forest characteristics relate to different levels of bird species richness between treatments, generalized linear models (GLMs) with a quasi-poisson distribution were fitted to account for overdispersion in count data (Warton et al., 2016). Species richness was set as the response variable, with structural predictors included total deadwood volume, basal area, and understory cover of both conifers and broadleaves. A full additive model, including all structural predictors and treatment as fixed effects, was fitted to provide a broad overview of the relationships between forest structure and species richness. Based on the most influential variables (deadwood volume, conifer basal area and broadleaf basal area), additional models were developed to explore whether the effects of these key structural features varied between treatments. The second model included all three key structural features, third model focused on the composition of basal area (conifer and broadleaf), and the last model, specifically assessed the effects of deadwood volume and conifer basal area. Multicollinearity was assessed using Variance Inflation Factors (VIF), with a threshold set at < 5, and residual deviance was used to evaluate model fit.

All statistical analyses were conducted in R version 2023.12.0+369 using Posit Software (formerly RStudio).

3. Results

Overall, forest structural features and bird communities showed variable responses to restoration treatments, with clearer effects observed in Hornsö than in Käringberget. Restoration promoted similarities between target and restored stands, while unrestored stands remained ecologically distinct. Some structural attributes, such as deadwood volume and conifer presence, consistently differed between treatments. Bird species richness and community composition showed limited responses, with only specific functional groups and indicator species reflecting treatment-related differences.

3.1 Forest structural complexity

3.1.1 Across treatments

In Hornsö, deadwood volume differed between treatments (x^2 = 10.22, df = 2, p = 0.006) with volumes significantly higher in the target stands compared to restored and unrestored ones (Figure 4a). Conifer occurence varied significantly across treatments (x^2 = 10.13, df = 2, p = 0.006), with higher proportions found in unrestored stands. In contrast, the composition of broadleaved tree species did not differ significantly between treatments (x^2 = 1.586, df = 2, p = 0.453) (Figure 5a). In Käringberget, I did not find any evidence for differences in deadwood volumes (x^2 = 1.82, df = 2, p = 0.403) (Figure 4b), broadleaved tree composition (x^2 = 0.14, df = 2, p = 0.932), or conifer tree composition, although a tendency was suggested (x^2 = 4.874, df = 2, p = 0.087) (Figure 5b). Despite being visually apparent, the differences did not reach statistical significance. However, broadleaved understory cover did differ between treatments, particularly between restored and unrestored stands (x^2 = 6.085, df = 2, p = 0.048). In general, the large standard deviation in Figure 4 and 5 indicates high variability among stands, suggesting that the data is widely spread around the mean. Appendices 6 - 8 provide detailed stand-level data on deadwood volumes, tree species, and understory composition, highlighting within-stand variation.

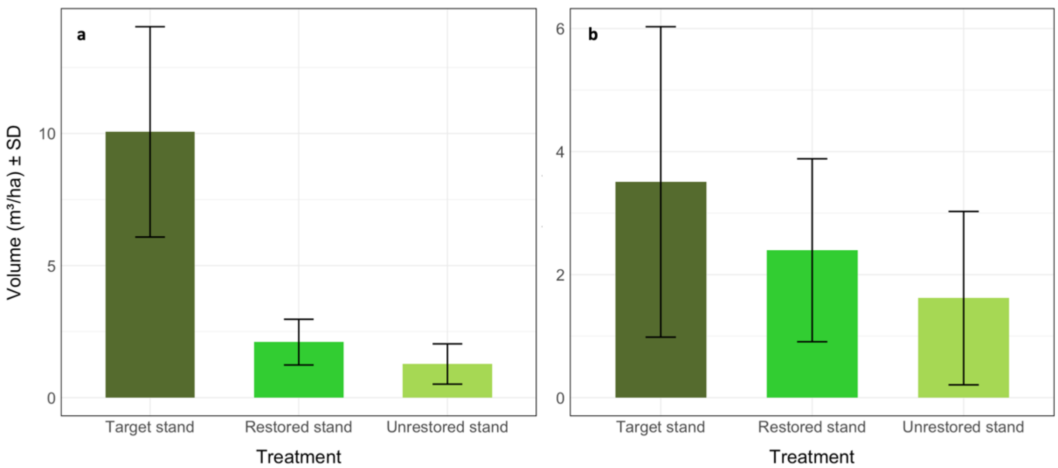


Figure 4: Deadwood volumes (m^3/ha) by treatment type. Panel (a) shows Hornsö, and panel (b) Käringberget.

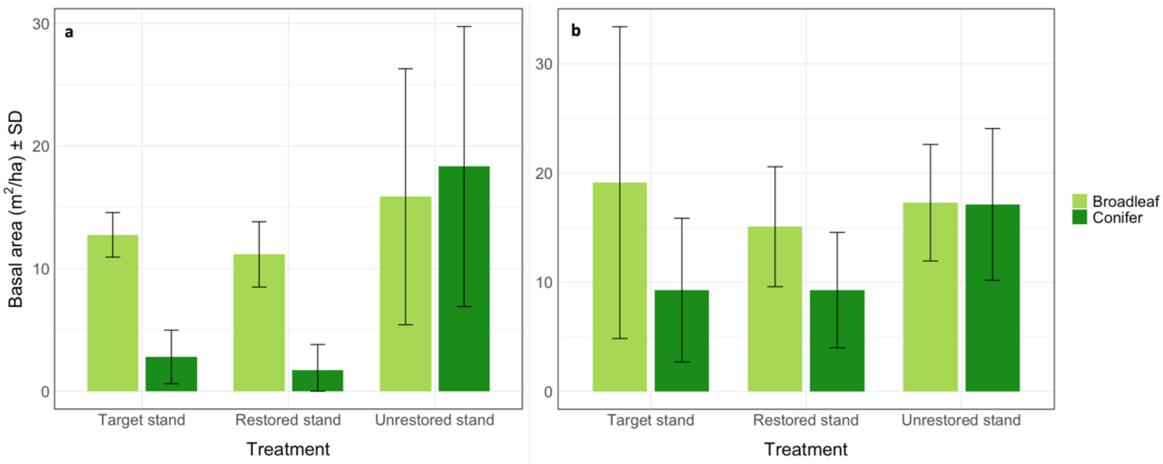


Figure 5: Basal area (m^2/ha) per tree category by treatment type. Panel (a) shows Hornsö, and panel (b) Käringberget.

3.1.2 Within treatments

Overall, forests structural composition in Hornsö differed significantly at the plot level (PERMANOVA: F = 15.29, R^2 = 0.304, p = 0.001), with treatment explaining approximately 30.4% of the variation (Figure 6a). Multivariate dispersion was homogeneous across treatments (F = 1.000, p = 0.401). When aggregating structural features per stand, the treatment effect became even stronger (F = 7.635, R^2 = 0.560, p = 0.001), with 56% of the variation explained by treatment (Figure 6b). Multivariate dispersion remained homogeneous across treatments (F = 0.129, p = 0.890). In contrast, Käringberget showed a statistically significant but weaker treatment effect at plot level (F = 3.147, R^2 = 0.080, p = 0.004), suggesting that only 8% of the variation is explained by treatment (Figure 6c). Dispersion remained homogeneous (F = 1.585, p = 0.198). When aggregating data per stand, the treatment effect was no longer significant (F = 1.196, R^2 = 0.166, p = 0.297), with 17% of variation explained, and no difference in dispersion was detected (F = 0.773, p = 0.487) (Figure 6d). The lack of significant differences in multivariate dispersion suggests that this pattern is not driven by unequal variability among treatments but by true compositional differences. Unrestored stands in both Hornsö and Käringberget were characterized by a higher basal area of coniferous trees, whereas target stands were associated with higher basal area of broadleaved species such as beech and oak in Hornsö, and birch in Käringberget, as indicated by the envfit vectors (Figure 6 a, c).

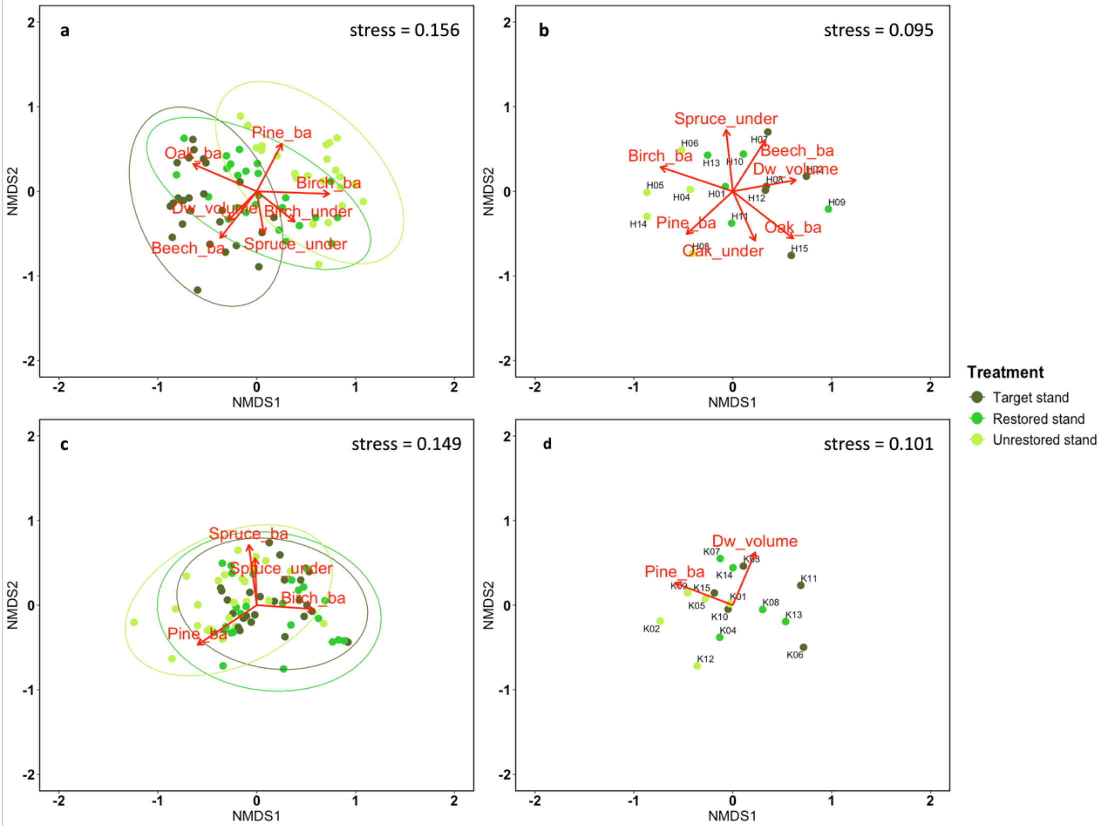


Figure 6: NMDS ordination of forest structural features by treatment. Panels a and b show the plot-level and stand-level ordinations for Hornsö, respectively; c and d show for Käringberget. Arrows from the envfit indicate which structural variables most strongly influence the positioning of the sites in ordination space. Colors represent the treatment type: dark green = target stand, medium green = restored stands, and the light green = unrestored stands. Ellipsoids illustrate the variability in structural composition within each treatment group.

3.2 Bird data

3.2.1 Bird species richness

Species richness did not differ significantly between treatments in Hornsö (ANOVA: $F = 1.721$, $p = 0.22$), although the effect size was small ($\eta^2 = 0.22$), suggesting that treatment might influence species richness, but the small sample size could restrict the ability to detect significant differences. Similarly, in Käringberget, no significant differences were found (ANOVA: $F = 1.993$, $p = 0.183$), although the moderate effect size ($\eta^2 = 0.27$). Bird species richness tended to differ between target and unrestored stands in Käringberget ($F = -1.86$, $p = 0.089$), indicating a potential reduction in species richness in unrestored stands (Figure 7).

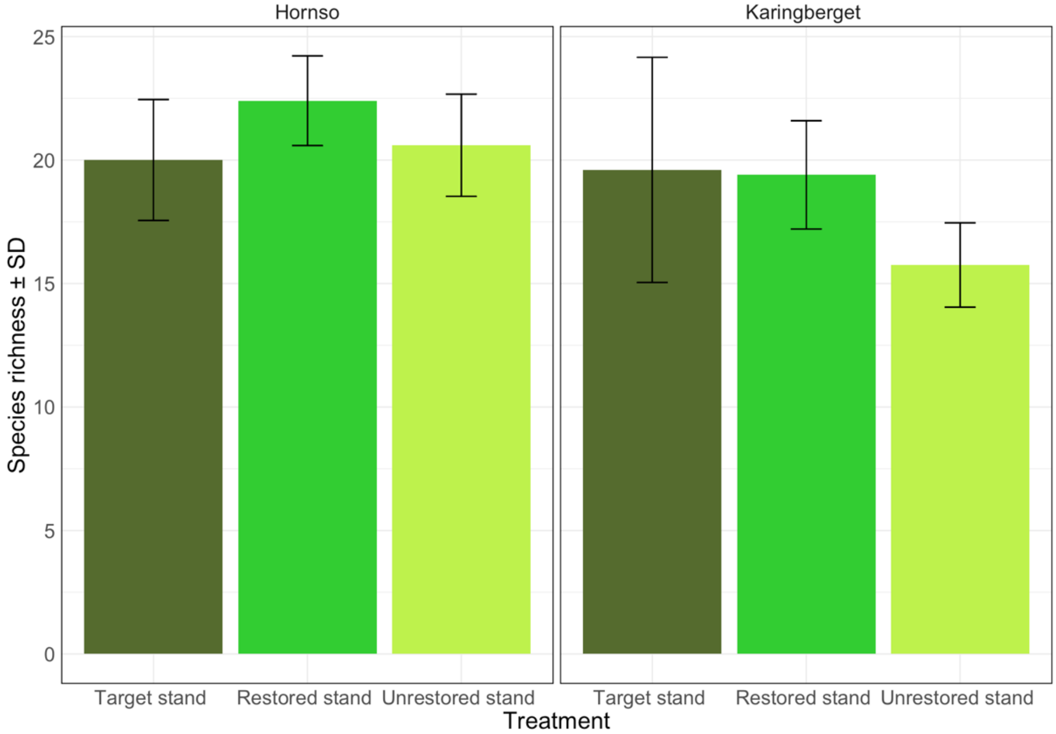


Figure 7: Mean (± standard deviation) of bird species richness across treatment types in the two study areas.

3.2.2 Community composition analysis

In Hornsö, I did not find any evidence for differences in bird community composition between treatments ($F = 0.654$, $R^2 = 0.098$, $p = 0.858$), with treatment explaining only 9.8% of the variation (Figure 8a). The majority of the variation (90.2%) was attributed to within-treatment variability or other unmeasured factors. The test for homogeneity of dispersion also revealed no significant differences ($F = 0.158$, $p = 0.849$), indicating similar variability within treatment groups. In Käringberget, bird assemblages likewise did not differ significanlty ($F = 1.175$, $R^2 = 0.176$, $p = 0.305$), although treatment accounted for a slightly higher proportion of variation (17.6%) compared to Hornsö (Figure 8b). Again, the dispersion test found no significant differences ($F = 0.461$, $p = 0.664$), indicating a consistent level of within-group variablility.

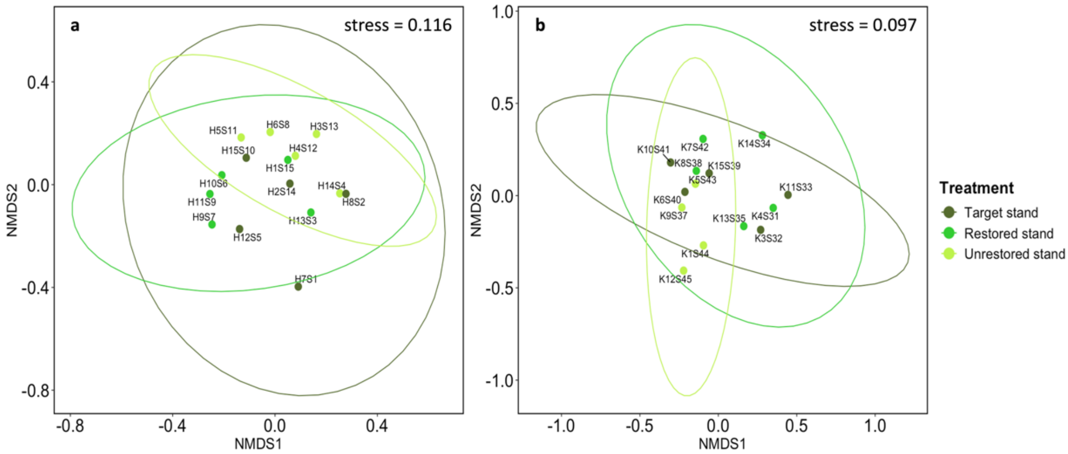


Figure 8: NMDS ordination showing bird community composition across treatment types. Each point represents a bird assemblage at a stand level. Colors indicate treatment: dark green = target stand, medium green = restored stand and light green = unrestored stand. Ellipsoids illustrate the variability in bird community composition within each treatment group.

3.2.3 Bird functional groups

In Hornsö, species richness differed among functional groups ($x^2 = 125.97$, df = 9, $p < 2.2e^{-16}$), suggesting that at least one functional group differs compared to the others (Appendix 9, Table 5). Groups with the highest mean across all stands were mature forest specialists, off-ground nesters and cavity nesters. In contrast, ground nesters and young mixed forest specialists had the lowest mean richness (Figure 9). Most functional groups did not differ between treatments, except bark feeders (Appendix 9, Table 7). Pairwise comparisons revealed that restored stands supported significantly higher bark feeders than in unrestored stands. In contrast, no differences were found between restored and target stands, nor between target and unrestored stands.

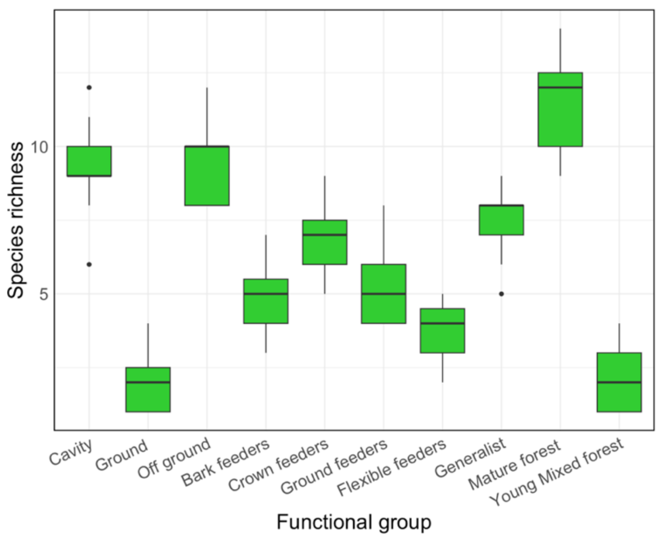


Figure 9: Variation in bird species richness across different functional groups in ecopark Hornsö, 2024. Statistical support provided in Appendix 9, Table 6.

A similarly strong pattern was observed in Käringberget, where species richness significantly differed among functional groups (x^2 = 111.99, df = 9, p < $2.2e^{-16}$), again suggesting variation in richness across groups (Appendix 10, Table 8). The highest mean values were found in off-ground nesters, mature forest specialists, and crown feeders. Bark feeders, flexible feeders, and young mixed forest specialists had the lowest richness (Figure 10). For most groups, species richness did not differ between treatments. However, ground nesters displayed a significant treatment effect. Both target and restored stands supported higher richness than unrestored stands, while no differences were found between target and restored stands. Flexbile feeders approached significance, showing a tendency for richness differences between target and unrestored stands. Additionally, generalist species exhibited lower richness in unrestored stands compared to target stands. No differences were found between target and restored stand or between restored and unrestored stands (see Appendix 10, Table 10).

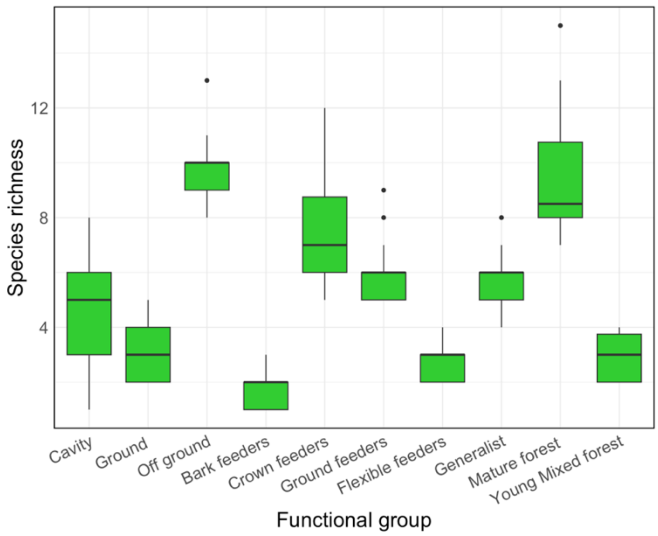


Figure 10: Variation in bird species richness across different functional groups in Käringberget, 2024. Statistical support provided in Appendix 10, Table 9.

3.2.4 Indicator species analysis

In Hornsö, the Eurasian nuthatch was identified as a significant indicator species for the target and restored stands. Other species like tree pipit, lesser spotted woodpecker, and crested tit also showed relatively high IndVal scores (above 0.6), even though their associations with specific treatment groups were not statistically significant (Appendix 11, Table 11). Similarly, in Käringberget, the tree pipit was also identified as a significant indicator species for the target and restored stands. The meadow pipit, associated with the restored treatment, nearly reached statistical significance and had a high IndVal score, suggesting a potential treatment association. Other species such as the spotted flycatcher, black woodpecker, and wood warbler also showed moderate IndVal but without statistical significance (Appendix 11, Table 12).

3.3 Relationship between structural complexity and species richness

In Hornsö, I did not find any evidence that bird species richness was related to structural forest characteristics. In Käringberget, bird species richness was positively associated with conifer basal area in target stands and was overall negatively associated with unrestored stands. Further, all three interaction models consistently showed bird species richness having a negative relation to conifer basal area in unrestored stands, meaning that species richness decreased with increasing conifer basal area. In the model assessing basal area composition, bird species richness was marginally positively associated with broadleafs in target stands. Deadwood volume was generally not significant on its own, but in the last model species richness increased with deadwood volume specifically in unrestored stands (Table 2). Other structural features, such as understory cover, showed no significant influence on species richness.

Table 2: GLM assessing the effects of forest structural features and treatment on bird species richness in Käringberget. Models use a quasi-poisson distribution. An asterisk (*) indicates a statistically significant ($p < 0.05$), while marginal significance ($0.05 < p < 0.1$) are indicated with a dot (.). *Abbreviations: DW_volume = deadwood volume, _ba = basal area, SE = standard error, Df = degrees of freedom. Model 1: full model; Model 2: key variables with treatments interactions; Model 3: basal area and treatment interactions; Model 4: deadwood volume and conifer basal area with treatment interaction.*

Model	Predictors	Estimate	SE	t-value	p-value	Null deviance	Residual deviance
Species_Richness	DW_volume	-0.022	0.029	-0.776	0.467	7.824 on 13 Df	1.646 on 6 Df
All variables	Conifer_ba	0.021	0.006	3.277	**0.017***		
	Broadleaf_ba	0.001	0.006	0.176	0.866		
	Conifer_under	0.034	0.087	0.391	0.710		
	Broadleaf_under	-0.003	0.045	-0.071	0.946		
	Restored stand	-0.028	0.099	-0.284	0.786		
	Unrestored stand	-0.444	0.121	-3.655	**0.011***		

Species_Richness (DW_volume + Conifer_ba + Broadleaf_ba) *Treatment	DW_volume	-0.009	0.023	-0.410	0.722	7.824 on 13 Df	0.154 on 6 Df
	Conifer_ba	0.034	0.006	5.373	**0.033***		
	Broadleaf_ba	0.004	0.004	1.072	0.396		
	Restored stand	0.185	0.339	0.545	0.641		
	Unrestored stand	0.451	0.424	1.063	0.399		
	DW_volume x Restored	0.007	0.053	0.124	0.912		
	DW_volume x Unrestored	0.144	0.068	2.123	0.168		
	Conifer_ba x Restored	-0.014	0.009	-1.458	0.282		
	Conifer_ba x Unrestored	-0.056	0.017	-3.247	*0.083.*		
	Broadleaf_ba x Restored	-0.004	0.014	-0.294	0.796		
	Broadleaf_ba x Unrestored	-0.011	0.012	-0.871	0.475		
Species_Richness (Conifer_ba + Broadleaf_ba) *Treatment	Conifer_ba	0.036	0.006	6.169	**0.002***	7.823 on 13 Df	0.517 on 5 Df
	Broadleaf_ba	0.006	0.002	2.158	*0.083.*		
	Restored stand	0.245	0.159	1.551	0.182		
	Unrestored stand	-0.101	0.281	-0.360	0.734		
	Conifer_ba x Restored	-0.016	0.008	-1.773	0.136		
	Conifer_ba x Unrestored	-0.027	0.009	-2.880	**0.035***		
	Broadleaf_ba x Restored	-0.005	0.007	-0.648	0.546		
	Broadleaf_ba x Unrestored	0.004	0.010	0.493	0.643		
Species_Richness (DW_volume + Conifer_ba) *Treatment	DW_volume	-0.030	0.011	-2.737	**0.041***	7.823 on 13 Df	0.264 on 5 Df
	Conifer_ba	0.029	0.004	8.314	**0.0004***		
	Restored stand	-0.008	0.084	-0.102	0.923		
	Unrestored stand	0.059	0.115	0.510	0.631		
	DW_volume x Restored	0.024	0.021	1.168	0.296		
	DW_volume x Unrestored	0.140	0.039	3.627	**0.015***		
	Conifer_ba x Restored	-0.009	0.006	-1.446	0.208		
	Conifer_ba x Unrestored	-0.044	0.009	-5.124	**0.004***		

4. Discussion

In this study, I combined field-based structural measurements and passive acoustic monitoring to assess how varying levels of forest restoration influence habitat complexity, bird species occurrence and the relationship among these in two different ecozones. My findings highlight three main patterns.

First, structural differences between treatments were more clearly expressed in Hornsö, where target stands showed the highest structural complexity, restored stands reflected intermediate conditions, and unrestored stands exhibited the lowest structural complexity. Whereas, in Käringberget, structural patterns categorisation was more subtle, likely due to higher within-stand variability. Second, while overall bird species richness did not differ between treatments, functional group and indicator species analysis revealed relevant patterns aligned with habitat features, indicating that specific structural elements influence bird assemblages. Third, the relationship between forest structure and bird richness was evident only in Käringberget. In this area, higher species richness was associated with greater basal area of both coniferous and broadleaved trees in target stands, while lower richness was linked to conifer dominance in unrestored stands. Deadwood volume also emerged as a key factor in structurally simpler areas.

Together, these findings underscore the importance of considering both structural and compositional aspects of habitat complexity when evaluating restoration outcomes and their ecological impacts.

4.1 Forest structural complexity across and within treatments

Overall, my results partly support the hypothesis that target and restored stands show greater structural complexity. However, restored stands appear to be a mix of unrestored and target conditions, rather than closely resembling target stands. Contrary to expectations, substantial within-stand variation suggests restoration is not applied uniformly, though some general treatment trends are still observable.

Deadwood is a structural feature widely recognized for its role in supporting forest-dwelling biodiversity. In managed forests, deadwood volumes are strongly shaped by the specific forest management practices implemented, as guided by management instructions and objectives (Bujoczek et al., 2020). With respect to my results, this suggests that the restoration practices applied have likely contributed to the differentiation in deadwood volume observed between treatments. Higher deadwood volume in target stands may lead to greater biodiversity potential, given the close link between deadwood, habitat availability and complexity (Siitonen, 2001). Both the amount and variety of deadwood are key components in sustainable forest management (De Zan et al., 2014). Additionally, deadwood volumes per stand rarely exceed $15m^3$/ha, suggesting that although variation is observed between treatment, the overall levels remain low. This underscores the need for increasing deadwood quantities more broadly across the landscape. Previous research by Siitonen (2001) and Müller and Bütler (2010) has identified a threshold of approximately 20-30m^3/ha of deadwood as critical for supporting the majority of saproxylic species in boreal coniferous forests. Natural forest reserves often contain 60-120 m^3/ha, whereas production forests typically hold lower volumes, often below 10 m^3/ha, highlighting the gap between current management practices and biodiversity needs.

Interestingly, in both ecoparks, broadleaved trees (as indicated by basal area (m^2/ha)) were generally more abundant than conifers across all treatments and sites. This pattern reflects the study design, which specifically selected stands dominated by deciduous species, aligned with the management goal of transitioning all stands toward conditons found in the target stands. Historically, southern areas like Hornsö shifted from hardwood to conifer dominance due to human land use (e.g., fire suppression, agriculture) and climate changes (Björse & Bradshaw,1998; Lindbladh & Bradshaw, 1998; Östlund et al., 1997; Sykes et al., 1996), while northern regions like Käringberget retained conifer dominance through 20th-century forestry favoring monocultures (Axelsson et al., 2002; Hellberg, 2004). This historical context explain why conifers may still be prominent in certain areas, despite the present-day abundance of broadleaves in the region. The relative broadleaves tree composition did not vary between treatments, possibly indicating that while restoration efforts may have promoted broadleaves, changes in both composition and abundance occur gradually over time (Östlund et al., 1997; Axelsson et al., 2002). However, broadleaf's understory cover of Käringberget was more developed in target and restored stands compared to unrestored ones. This may suggest that restoration indeed has started to promote understory regeneration of broadleaved species**,** an ecologically important component, as changes in this layer can influence forest recovery and productivity by acting as a source of new growing stock (Metzger & Schultz, 1984; Tappeiner & Alaback, 1989; Burke et al., 2008, Hekkala et al., 2014). In contrast, unrestored stands contained more conifers than target and restored ones, reflecting past silvicultural practices that favored conifers over broadleaves (Götmark et al., 2005). The reduced conifer dominance in target and restored stands suggests that restoration efforts can effectively shift trees composition toward greater structural heterogeneity and broadleaf presence (Larson et al., 2012).

In both Hornsö and Käringberget, structural variation within stands was evident, with plots differing in deadwood volume and the dominance of certain tree species, contributing to local-scale heterogeneity within stands. Despite this within-stand variation, results demonstrate a clear effect of management treatment on forest structural composition in Hornsö (but not in Käringberget). These results suggest that treatment-related structural differences are more apparent at broader spatial scales, likely reflecting cumulative effects of management across all plots and stands. Interestingly, restored stands appeared structurally more similar to unrestored once in terms of deadwood characteristics, while tree species composition more closely resembled that of target stands. This pattern supports the idea that restored stands function as transitional areas-partially retaining features of unrestored conditions while gradually developing attributes associated with target stands, as seen by Atkinson et al. (2022).

An important finding in my work is that the differences across stands and ecoparks underscore the variable outcomes of management interventions. While restoration is being applied coherently to guild forests toward desired conditions, such disparities demonstrate that it is not an one-size-fits-all process; rather, it is shaped by historical management, local environmental conditions, and broader ecological contexts, as shown by Bujoczek et al. (2020). However, the application of fixed treatment categories (target, restored, unrestored) may oversimplify or overestimate an ecological reality. Instead of categorical differences, considering gradual changes might be more appropriate within restoration work (Atkinson et al. 2022). Each stand and ecopark has its own legacy, management timeline, structural characteristics and objectives, making such categorical labels insufficient to capture the nuances of restoration process with respect to habitat complexity. As demonstrated by Munteanu et al. (2015), historical land use can leave strong legacy effects, with long-lasting impacts on ecosystems that influence forest structure and disturbance regimes for centuries. This calls for a more nuanced classification system; one that is more context-dependent, stand-specific or structure-specific. Further, establishing ecological baselines, both pre- and post-restoration, would also improve the capacity to track progress and inform adaptive management strategies.

4.2 Bird species richness, community composition and their relationships with forest structure

Overall, my results show no differences in bird species richness, species composition or community dispersion across treatments in either ecopark. This suggest that bird assemblages are relatively resilient to the structural changes introduced by restoration efforts at the time of investigation. Consequently, these findings do not support my initial hypothesis. Previous research has shown that vegetation structure is a critical component of forest health and a key driver of species assemblages (Trumbore et al., 2015). The lack of observed differences might imply that current forest management interventions have not yet resulted in sufficient structural differentiation, or that high variation among stands within treatments may have obscured clear distinctions in community composition. Structural features such as mature trees, canopy cover, the density of seedlings and saplings play an important role in shaping preferences of vertebrate species in forests (Kreurzweiser et al., 2020). Many species depend on wooded vegetation for food, shelter and breeding (Larrieu et al., 2014). It is also possible that more complex structural features or simply a greater quantity of existing features would be necessary to detect changes in community composition. Additionally, spatial context, forest connectivity, and the ecological quality of surrounding areas can significantly affect the perceived and actual value of a given stand. As shown by Hekkala et al. (2023), Kallimanis et al. (2008), and Whittaker et al. (2001), forest heterogeneity and the availability of habitat over larger areas often amplify biodiversity outcomes. In this sense, some stands may hold greater or lesser ecological value depending on their surroundings or individual size. However, this remains uncertain due to the lack of data on the structural condition of nearby forests.

Notably, and in support of my hypothesis, clearer patterns emerged when analyzing functional bird groups. These groups offered detailed insights into species presence and responses to forest conditions, revealing a general pattern across the study areas. These differences highlight the varying habitat preferences and structural dependencies among bird groups. Traits, defined as any morphological, physiological or phenological characteristics measurable at the individual level (Díaz & Cabido, 2001), play a crucial role in habitat selection and influence how species respond to different forest structures. The presence or absence of a certain species or group can serve as indicators of baseline environmental conditions and help assess the extent to which communities are influenced by environmental changes (Gumede et al., 2022).

For instance, the presence of species associated with mature forests suggests that some stands may already support well-developed structural features, aligning with findings that mature forests, with their large, old trees, and substantial deadwood volumes, provide key conditions for specialized species (Bergner et al., 2015; Nikolov, 2008). Such forests contribute to small-scale environmental heterogeneity and create a diverse set of structural characteristics (Kuuluvainen, 2002; Balestrieri et al., 2015), which in turn support the presence of off-ground, cavity nesting and crown feeding birds. Additionally, the low richness of early successional species supports the idea that the forest stands in both ecoparks more closely resemble mature forest conditions. The observed richness of cavity nesters in Hornsö may reflect the availability of suitable deadwood in terms of both quantity and quality, consistent with findings that deadwood provides critical habitat for many organisms, including top predators like woodpeckers (Tranberg et al., 2024; Siitonen, 2001). In contrast, bark feeders were notably less represented in unrestored stands, likely due to a lack of suitable foraging substrates such as high-quality deadwood with intact bark (Whelan & Maina, 2005).

The situation in Käringberget presents another layer of complexity. Both cavity nesters and bark feeders exhibit lower richness across all stands, suggesting poorly developed deadwood conditions, a conclusion supported by field observations. Ground nesting birds also show low richness, likely due to suboptimal ground level conditons. Given that nest failure among ground nesters is often linked to high predation pressure (Shipley et al., 2013), it is possible that these forests lack the dense vegetation or hiding spots required to protect nests, further limiting these species success. Richness is especially lower in the unrestored stands. Generalist species showed higher richness in target stands compared to unrestored ones, suggesting that Käringberget may lack the specific structural features required by more specialized birds and instead provide more uniform habitat that favor generalist species (Hinsley et al., 2009; Öckinger et al., 2010; Dondina et al., 2015; Porro et al., 2019). Even flexible feeders, typically less dependent on specific habitat structures, showed higher richness in the target stands. Although both generalists and flexible feeders are poorly represented, their greater richness in target stands may indicate that key habitat requirements are better fulfilled for a wider range of species under the target treatments. Overall, the observed patterns likely reflect how landscape configuration and resource availability, shape colonization, dispersal, and comunity composition (Fahrig, 2002; Kupfer et al., 2006; Niebuhr et al., 2015; Gumede et al., 2022). Trends among functional groups support the idea that structural complexity is a key driver of bird assemblages, shaping species interactions and filtering communities based on ecological traits (Lavorel et al., 2007; Biswas & Mallik, 2011). It further also reinfornced the structural contrast between target, restored and unrestored stands within the same area.

The influence of forest structures on bird communities showed contrasting patterns between the two ecoparks. No clear relationship was found in Hornsö, which may suggest that the measured forest attributes do not strongly influence bird communities. This absence of effect could indicate that other unmeasured factors are playing a larger role in shaping avian assemblages. In Käringberget, bird species richness was positively associated with conifer basal area in target stands, suggesting that coniferous trees can provide valuable habitat features when embedded within a structurally complex environment. This aligns with findings from Juchheim et al. (2020), who showed a link between stand structural complexity and tree species diversity. However, this relationship shifted in unrestored stands, where lower species richness was associated with higher conifer dominance, likely due to simplified structures that reduce habitat quality and resource availability (Felton et al., 2021). Bird species richness showed a marginally positive association with broadleaf basal area in target stands, indicating that promoting mixed-species forests may help mitigate biodiversity loss and enhance ecosystem services (Huuskonen et al., 2020; Felton et al., 2021). Although deadwood volume did not show consistent effect overall, species richness was positively associated with deadwood volumes in unrestored stand, supporting the idea that deadwood can enhance biodiversity in structurally poorer habitats (Bujoczek et al., 2020).

4.3 Indicator species as reflections of ecological conditions and site associations

Indicator species are selected based on their ability to reflect the biotic or abiotic state of the environment. This method helps identify individual species that are strongly associated with particular habitat types (Severns & Sykes, 2020). While community-wide differences may be subtle, indicator species analysis did reveal fine-scale responses to restoration measures that where not apparent at the assemblage level. This supported my hypothesis that certain species are closely associated with specific treatment types. The Eurasian nuthatch serves as a clear example, emerging as a significant indicator species for target and restored stands in Hornsö. This species is a bark feeder and cavity nester, closely tied to mature, structurally complex forests, often preferring area with broadleaved trees (especially oak trees) and ample deadwood (Matthysen & Adriaensen, 1998; Dondina et al., 2015; Porro et al., 2019). The presence of the Eurasian nuthatch as an indicator species suggests that restoration is successfully fostering key forest attributes (e.g., deadwood presence, tree diversity) that favours the presence of the Eurasian nuthatch (Matthysen et al., 1995; Bellamy et al., 1998).

In Käringberget, the tree pipit was identified as an indicator species for target and restored stands, and was largely absent from unrestored stands. The tree pipit is a ground feeder and nester, and is classified as a generalist (Mikusinski et al., 2018; Versluijs et al., 2020). The tree pipit typically avoids stands with heterogeneous tree age structure and prefers areas, with relatively high canopy openness, low shrub density, and a dense field layer (Loske, 1987). In conclusion, this analysis emphasizes that restoration can enhance habitat quality in ways that benefits indicator species, even if broader community shifts are not yet strongly apparent. These findings also align with differences observed across functional groups, reinforcing the idea that structural restoration is already benefiting species with specific ecological requirements.

4.4 Regional consistency in bird assemblage responses to restoration

My findings show that bird assemblage responses to restoration efforts are not fully consistent across regions. This challenges my initial hypothesis that similar restoration efforts would be observed across sites. In Käringberget restoration appears to be less uniformly implemented, possibly due to environmental variability, differing baseline conditions or a longer time frame for impacts to become apparent. It is also possible that of Hornsö's overall condition is more advanced than Käringberget's, making restoration measures appear less effective. Given that forest structural complexity is known to influence species and trait diversity (Massicott et al., 2013; Biswas et al., 2018), this implies that regional variation in forest structure may generate unique bird responses in each ecopark.

Numerous taxonomic groups, including bird, mammals, fish, etc. exhibit geographic patterns in their biological variation (McCain, 2005; Brown, 2013; Loewen et al., 2022; Terborgh, 1977). Therefore, bird responses to restoration cannot be generalized. As demonstrated by Hewitt and Cummings (2012), restoration outcomes are strongly context-dependent. The comparison may be limited in relevance, as only one site represents each ecozone. Including additional sites could help reveal clearer spatial patterns and provide a more robust foundation for future research on regional differences.

4.5 General implications and limitations

Species richness represents a measure of species variety, based simply on counting the number of species in a given sample (Kiester, A., 2013). While it is commonly used as an indicator of biodiversity, it has limitations (Gotelli & Colwell, 2001; Magurran, 2004, Chase & Knight, 2013). Relying solely on richness can underestimate the scale of biodiversity change, as it often fails to capture species turnover or underlying ecological dynamics. Therefore, trends in species richness may not accurately reflect the outcomes of conservation or management actions (Hillebrand, et al., 2017; Fedor & Zvaríková, 2019; Jarrett & Willis, 2024). As this study focused on species richness, the findings likely reflect variations in habitat and community structure rather than absolute species abundance. Interpretation should be approached with caution, acknowledging that more complex dynamics are likely present but not fully explored. For these reasons, a more comprehensive dataset, including measures such as α- and β- diversity, species abundance or other community-level indicators, would provide greater insight into biodiveristy differences.

One possible extension of this research would be to incorporate methods that estimate territory or species density based on vocal activity. Various approaches have been developed that use the frequency of calls or detections per recording period at a single point as proxies for territory density. Among these, the most widely used is the vocal activity rate, which calculates the number of calls per time unit (Pérez-Granados & Traba, 2021). A related method is the detection rate, which quantifies how often a species vocalization is detected, typically using automated classifiers, within specific time intervals, regardless of the number of individual calls (Hutschenreiter et al., 2024). Additionally, species richness is sensitive to sampling effort, increased sampling effort often leads to higher observed richness values (Azovsky, 2011; Fedor & Zvarìková, 2019). The relatively small sample size (n = 5) may have limited the ability to detect broader patterns. Another important extension of this research would be to incorporate pre- and post-restoration data, enabling a more robust evaluation of treatment effects and potentially provide a clearer representation of how bird communities respond to restoration over time.

An important consideration with passive acoustic monitoring is that the distance between a vocalizing bird and the recording device can significantly affect the detection probability (Winiarska et al., 2024). Some bird species produce loud, far-carrying calls that can be detected from considerable distances, while others emit softer calls that are only recorded when the bird is in close proximity to the recorder. This variation can introduce detection biases, with distant individuals potentially underrepresented due to sound attenuation (Jarrett & Willis, 2024). Background noise, overlapping bird songs and the structural openness of the forest can all influence sounds transmission and detection range, potentially causing variation in detectability across recordings and forest stands (Haupert et al., 2022; Winiarska et al., 2024). Another important factor to consider is the home range size and movement patterns of different bird species. Highly mobile species or those with large territories may be detected by multiple recording units. This can lead to inflated detection rates and potential pseudoreplication, especially in forest stands that are close to one another. As a result, some detections may not be independent, which is crucial to consider when comparing bird assemblages.

Moreover, the spatial context of each stand, including the surrounding forest and landscape features, can influence bird community composition. The quality and structure of adjacent habitats may attract additional species, contributing to higher diversity within a stand. This landscape-level habitat heterogeneity, defined by variation in structural complexity, resource availability, and niche diversity, is often positively correlated with species richness (Hekkala et al., 2023). Additionally, the species-area relationship indicate that species richness increases with habitat area (Sand-Jensen, 2001; Lewinsohn & Jorge, 2023; Connor & McCoy, 2023). Therefore, I suggest future research to consider both the internal characteristics of stands and their broader landscape context when interpreting patterns of bird diversity based on acoustic data.

5. Conclusion

This study highlights how forest restoration efforts have begun to shape structural and avian community characteristics, though with varying outcomes across our ecoparks and treatments. Deadwood volumes were highest in target stands, with restored and unrestored stands showing similar lower levels. Broadleaved trees dominated across all treatments, and conifers were more abundant in unrestored stands. In Hornsö, treatment-related structural differences were evident at the stand level, with restored stands functioning as transitional stages between unrestored and target conditions. By contrast, Käringberget exhibited more subtle trends, likely due to higher within-stand variability and heterogeneous restoration conditions, resulting in less distinct treatment effects. Structural variation within stands was pronounced, suggesting that treatment categories (target, restored, unrestored) may oversimplify a more complex ecological reality. These patterns highlight the ongoing nature of restoration in our study area, in which structural and compositional changes may progress at different rates.

Bird species richness did not differ between treatment, yet functional group analysis revealed patterns aligned with structural features. Variation within a functional group across treatments was observed, with higher richness and the presence of strong indicator species primarily associated with target and restored stands, suggesting a preference of these conditions over those found in unrestored stands. This pattern may reflect the presence of key structural features already influencing species occurrence and habitat selection. The influence of forest structure on bird communities was most apparent in Käringberget, where features like deadwood volumes and conifer basal area were closely linked to bird diversity and habitat use. This suggests that increasing structural heterogeneity and key habitat features could boost species richness in unrestored areas. These findings highlight that the ecological role of specific forest components depends on the broader structural context, underscoring the need to consider all habitat features collectively.

While restoration has not yet led to clear shifts in overall avain richness, it appears to benefit species with specific ecological requirements. However, limitations in sample size, passive acoustic monitoring, and the lack of spatial forest context constrain broader interpretations. To fully understand restoration outcomes, future research should adopt more nuanced, stand-specific approach that considers forest legacy, management timeline, structural characteristics and objectives. Complementing structural indicators with data on, α- & β-diversity, species abundance, community-level indicator, food availability, canopy age and density, live tree biomass, forest continuity and a deeper understanding of understory cover would strengthen assessments of biodiversity recovery and bird community responses in our study area.

References

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Anderson, M. J. (2005). Distance-Based tests for homogeneity of multivariate dispersions. *Biometrics*, *62*(1), 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, *9*(6), 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Atkinson, J., Brudvig, L. A., Mallen-Cooper, M., Nakagawa, S., Moles, A. T. & Bonser, S. P. (2022). Terrestrial ecosystem restoration increases biodiversity and reduces its variability, but not to reference levels: A global meta-analysis. *Ecology Letters*, *25*(7), 1725–1737. https://doi.org/10.1111/ele.14025

Azovsky, A. I. (2011). Species-area and species-sampling effort relationships: disentangling the effects. *Ecography*, *34*(1), 18–30. http://www.jstor.org/stable/41239238

Balestrieri, R., Basile, M., Posillico, M., Altea, T., De Cinti, B., & Matteucci, G. (2015). A guild-based approach to assessing the influence of beech forest structure on bird communities. *Forest Ecology and Management*, *356*, 216–223. https://doi.org/10.1016/j.foreco.2015.07.011

Basel, M., Storch, I. & Mikusiński, G. (2021). Abundance, species richness, and diversity of forest bird assemblages – The relative importance of habitat structures and landscape context. *Ecological Indicators*, 133, 108402. https://doi.org/10.1016/j.ecolind.2021.108402.

Basile, M., Valerio, F., Balestrieri, R., Posillico, M., Bucci, R., Altea, T., De Cinti, B., & Matteucci, G. (2016). Patchiness of forest landscape can predict species distribution better than abundance: the case of a forest-dwelling passerine, the short-toed treecreeper, in central Italy. *PeerJ*, *4*, e2398. https://doi.org/10.7717/peerj.2398

Beason, R. D., Riesch, R. & Koricheva, J. (2023). Investigating the effects of tree species diversity and relative density on bird species richness with acoustic indices. *Ecological Indicators*, 141, 109111. https://doi.org/10.1016/j.ecolind.2022.109111.

Bellamy, P. E., Brown, N. J., Enoksson, B., Firbank, L. G., Fuller, R. J. & Schotman, S. H. (1998). The Influences of Habitat, Landscape Structure and Climate on Local Distribution Patterns of the Nuthatch (Sitta europaea L.). *Oecologia*, *115*(1/2), 127–136. https://www.jstor.org/stable/4221987

Bergner, A., Avcı, M., Eryiğit, H., Jansson, N., Niklasson, M., Westerberg, L., & Milberg, P. (2015). Influences of forest type and habitat structure on bird assemblages of oak (Quercus spp.) and pine (Pinus spp.) stands in southwestern Turkey. *Forest Ecology and Management*, *336*, 137–147. https://doi.org/10.1016/j.foreco.2014.10.025

BirdLife International. (2024). *Species factsheets*. BirdLife webpage. https://datazone.birdlife.org/species/factsheet/black-headed-gull-larus-ridibundus

Biswas, S. R. & A. U. Mallik. (2011). Species diversity and functional diversity relationship varies with disturbance intensity. Ecosphere 2(4):art52. https://doi.org/10.1890/ES10-00206.1

Biswas, S. R., Mallik, A. U., Braithwaite, N. T. & Biswas, P. L. (2018). Effects of disturbance type and microhabitat on species and functional diversity relationship in stream-bank plant communities. *Forest Ecology and Management*, *432*, 812–822. https://doi.org/10.1016/j.foreco.2018.10.021

Björse, G., & Bradshaw, R. (1998). 2000 years of forest dynamics in southern Sweden:

suggestions for forest management. *Forest Ecology and Management*, *104*(1–3), 15–26. https://doi.org/10.1016/s0378-1127(97)00162-x
Bradfer-Lawrence, T., Gardner, N., Willis, S. G., Dent, D. H., Bunnefeld, L. & Bunnefeld, N. (2019). Guidelines for the use of acoustic indices in environmental research. *Methods in Ecology and Evolution*, 10(10), 1796–1807. https://doi.org/10.1111/2041-210X.13254.
Brown, J. H. (2013). Why are there so many species in the tropics? *Journal of Biogeography*, *41*(1), 8–22. https://doi.org/10.1111/jbi.12228
Brumelis, G., Jonsson, B., Kouki, J., Kuuluvainen, T., & Shorohova, E. (2011). Forest naturalness in northern Europe: perspectives on processes, structures and species diversity. *Silva Fennica*, *45*(5). https://doi.org/10.14214/sf.446
Bujoczek, L., Bujoczek, M. & Zięba, S. (2020). How much, why and where? Deadwood in forest ecosystems: The case of Poland. *Ecological Indicators*, *121*, 107027. https://doi.org/10.1016/j.ecolind.2020.107027
Bujoczek, L., Bujoczek, M., & Zięba, S. (2021). Distribution of deadwood and other forest structural indicators relevant for bird conservation in Natura 2000 special protection areas in Poland. *Scientific Reports*, *11*(1). https://doi.org/10.1038/s41598-021-94392-1
Burivalova, Z., Towsey, M., Boucher, T., Truskinger, A., Apelis, C., Roe, P. & Game, E. (2017). Using soundscapes to detect variable degrees of human influence on tropical forests in Papua New Guinea. *Conservation Biology*, 32, 205–215. https://doi.org/10.1111/cobi.12968.
Burivalova, Z., Game, E. T., & Butler, R. A. (2019). The sound of a tropical forest. *Science*, *363*(6422), 28–29. https://doi.org/10.1126/science.aav1902
Burke, D. M., Elliott, K. A., Holmes, S. B., & Bradley, D. (2008). The effects of partial harvest on the understory vegetation of southern Ontario woodlands. *Forest Ecology and Management*, *255*(7), 2204–2212. https://doi.org/10.1016/j.foreco.2007.12.032
Caprio, E., Ellena, I. & Rolando, A. (2008). Assessing habitat/landscape predictors of bird diversity in managed deciduous forests: a seasonal and guild-based approach. *Biodiversity and Conservation*, *18*(5), 1287–1303. https://doi.org/10.1007/s10531-008-9478-1
CBD (Convention on Biological Diversity), (2010). COP 10 Decision X/2: Strategic Plan for Biodiversity 2011–2020. http://www.cbd.int/decision/cop/?id=12268
Chase, J. M. & Knight, T. M. (2013). Scale-dependent effect sizes of ecological drivers on biodiversity: Why standardised sampling is not enough. *Ecology Letters*, 16, 17–26.
Connor, E. F. & McCoy, E. D. (2023). Species–Area relationships. In *Elsevier eBooks* (pp. 361–377). https://doi.org/10.1016/b978-0-12-822562-2.00074-8
Czeszczewik, D., Zub, K., Stanski, T., Sahel, M., Kapusta, A., & Walankiewicz, W. (2014). Effects of forest management on bird assemblages in the Bialowieza Forest, Poland. *iForest - Biogeosciences and Forestry*, *8*(3), 377–385. https://doi.org/10.3832/ifor1212-007
De Cáceres, M. & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, *90*(12), 3566–3574. https://doi.org/10.1890/08-1823.1
De Zan, L. R., Battisti, C., & Carpaneto, G. (2014). Bird and beetle assemblages in relict beech forests of central Italy: a multi-taxa approach to assess the importance of dead wood in biodiversity conservation. *Community Ecology*, *15*(2), 235–245. https://doi.org/10.1556/comec.15.2014.2.12
DíAz, S. & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*(11), 646–655. https://doi.org/10.1016/s0169-5347(01)02283-2
Dondina, O., Orioli, V., Massimino, D., Pinoli, G. & Bani, L. (2015). A method to evaluate

the combined effect of tree species composition and woodland structure on indicator birds. *Ecological Indicators*, *55*, 44–51. https://doi.org/10.1016/j.ecolind.2015.03.007

Dröge, S., Martin, D. A., Andriafanomezantsoa, R., Burivalova, Z., Fulgence, T. R., Osen, K., Rakotomalala, E., Schwab, D., Wurz, A., Richter, T., & Kreft, H. (2020). Listening to a changing landscape: Acoustic indices reflect bird species richness and plot-scale vegetation structure across different land-use types in north-eastern Madagascar. *Ecological Indicators*, *120*, 106929. https://doi.org/10.1016/j.ecolind.2020.106929

Eglington, S. M., Noble, D. G., & Fuller, R. J. (2012). A meta-analysis of spatial relationships in species richness across taxa: Birds as indicators of wider biodiversity in temperate regions. *Journal for Nature Conservation*, *20*(5), 301–309. https://doi.org/10.1016/j.jnc.2012.07.002

Fahrig, L. (2002), effect of habitat fragmentation on the extinction threshold: A synthesis. Ecological Applications, 12: 346-353. https://doi.org/10.1890/1051-0761(2002)012[0346:EOHFOT]2.0.CO;2

Fedor, P. & Zvaríková, M. (2019). Bildiversity Indices. In B. Fath (Ed.), Encyclopedia of Ecology. (2nd Ed., pp. 337-346). Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.10558-5.

Felton, A., Hedwall, P., Trubins, R., Lagerstedt, J., Felton, A., & Lindbladh, M. (2021). From mixtures to monocultures: Bird assemblage responses along a production forest conifer-broadleaf gradient. *Forest Ecology and Management*, *494*, 119299. https://doi.org/10.1016/j.foreco.2021.119299

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global consequences of land use. Science 309, 570–574.

Fridman, J., & Walheim, M. (2000). Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management*, *131*(1–3), 23–36. https://doi.org/10.1016/s0378-1127(99)00208-x

Gibb, R., Browning, E., Glover-Kapfer, P. & Jones, K. E. (2018). Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods in Ecology and Evolution*, *10*(2), 169–185. https://doi.org/10.1111/2041-210x.13101

Gotelli, N. J. & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Götmark, F., Fridman, J., Kempe, G., & Norden, B. (2005). Broadleaved tree species in conifer-dominated forestry: Regeneration and limitation of saplings in southern Sweden. *Forest Ecology and Management*, *214*(1–3), 142–157. https://doi.org/10.1016/j.foreco.2005.04.001

Gregory, R. D., & Van Strien, A. (2010). Wild Bird Indicators: Using composite population trends of birds as measures of environmental health. *ORNITHOLOGICAL SCIENCE*, *9*(1), 3–22. https://doi.org/10.2326/osj.9.3

Gumede, S. T., Smith, D. a. E., Ngcobo, S. P., Sosibo, M., Smith, Y. C. E. & Downs, C. T. (2022). The influence of forest characteristics on avian species richness and functional diversity in Southern Mistbelt Forests of South Africa. *Global Ecology and Conservation*, *34*, e02047. https://doi.org/10.1016/j.gecco.2022.e02047

Halme, P., Allen, K. A., Auniņš, A., Bradshaw, R. H., Brūmelis, G., Čada, V., Clear, J. L., Eriksson, A., Hannon, G., Hyvärinen, E., Ikauniece, S., Iršėnaitė, R., Jonsson, B. G., Junninen, K., Kareksela, S., Komonen, A., Kotiaho, J. S., Kouki, J., Kuuluvainen, T., . . . Zin, E. (2013). Challenges of ecological restoration: Lessons from forests in northern Europe. *Biological Conservation*, *167*, 248–256. https://doi.org/10.1016/j.biocon.2013.08.029

Hämäläinen, A., Strengbom, J., & Ranius, T. (2018). Conservation value of low-productivity forests measured as the amount and diversity of dead wood and saproxylic beetles. *Ecological Applications*, *28*(4), 1011–1019. https://doi.org/10.1002/eap.1705

Haupert, S., Sèbe, F. & Sueur, J. (2022). Physics-based model to predict the acoustic detection distance of terrestrial autonomous recording units over the diel cycle and across seasons: Insights from an Alpine and a Neotropical forest. *Methods in Ecology and Evolution*, *14*(2), 614–630. https://doi.org/10.1111/2041-210x.14020

Hekkala, A., Tarvainen, O., & Tolvanen, A. (2014). Dynamics of understory vegetation after restoration of natural characteristics in the boreal forests in Finland. *Forest Ecology and Management*, *330*, 55–66. https://doi.org/10.1016/j.foreco.2014.07.001

Hekkala, A., Jönsson, M., Kärvemo, S., Strengbom, J., & Sjögren, J. (2023). Habitat heterogeneity is a good predictor of boreal forest biodiversity. *Ecological Indicators*, *148*, 110069. https://doi.org/10.1016/j.ecolind.2023.110069

Hellberg, E. (2004). Historical variability of deciduous trees and deciduous forests in Northern Sweden. Effect of forest fires, land-use and climate. (Doctoral thesis, Swedish University of Agricultural Sciences).

Hewitt, J., & Cummings, V. (2012). Context-dependent success of restoration of a key species, biodiversity and community composition. *Marine Ecology Progress Series*, *479*, 63–73. https://doi.org/10.3354/meps10211

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., Filstrup, C. T., Harpole, W. S., Hodapp, D., Larsen, S., Lewandowska, A. M., Seabloom, E. W., Van de Waal, D. B. & Ryabov, A. B. (2017). *Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring*. Journal of Applied Ecology, 55(1), 169–184. https://doi.org/10.1111/1365-2664.12959

Hinsley, S. A., Hill, R. A., Bellamy, P., Broughton, R. K., Harrison, N. M., Mackenzie, J. A., Speakman, J. R., & Ferns, P. N. (2009). Do Highly Modified Landscapes Favour Generalists at the Expense of Specialists? An Example using Woodland Birds. *Landscape Research*, *34*(5), 509–526. https://doi.org/10.1080/01426390903177276

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, *24*(11), 599–605. https://doi.org/10.1016/j.tree.2009.05.012

Hutschenreiter, A., Andresen, E., Briseño-Jaramillo, M., Torres-Araneda, A., Pinel-Ramos, E., Baier, J., & Aureli, F. (2024). How to count bird calls? Vocal activity indices may provide different insights into bird abundance and behaviour depending on species traits. *Methods in Ecology and Evolution*, *15*(6), 1071–1083. https://doi.org/10.1111/2041-210x.14333

Huuskonen, S., Domisch, T., Finér, L., Hantula, J., Hynynen, J., Matala, J., Miina, J., Neuvonen, S., Nevalainen, S., Niemistö, P., Nikula, A., Piri, T., Siitonen, J., Smolander, A., Tonteri, T., Uotila, K., & Viiri, H. (2020). What is the potential for replacing monocultures with mixed-species stands to enhance ecosystem services in boreal forests in Fennoscandia? *Forest Ecology and Management*, *479*, 118558. https://doi.org/10.1016/j.foreco.2020.118558

IPBES. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (S. Díaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, et al., Eds.). IPBES Secretariat.

Jackson, S. T., & Hobbs, R. J. (2009). Ecological restoration in the light of ecological history. *Science*, *325*(5940), 567–569. https://doi.org/10.1126/science.1172977

Jarrett, D. & Willis, S. G. (2024). Acoustic detection rate can outperform traditional survey approaches in estimating relative densities of breeding waders. *Ibis*. https://doi.org/10.1111/ibi.13375

John, C. Tappeiner II and Paul B. Alaback. (1989). Early establishment and vegetative growth of understory species in the western hemlock – Sitka spruce forests of southeast Alaska. *Canadian Journal of Botany*. **67**(2): 318-326. https://doi.org/10.1139/b89-046
Juchheim, J., Ehbrecht, M., Schall, P., Ammer, C., & Seidel, D. (2020). Effect of tree species mixing on stand structural complexity. *Forestry an International Journal of Forest Research*. https://doi.org/10.1093/forestry/cpz046
Kallimanis, A. S., Mazaris, A. D., Tzanopoulos, J., Halley, J. M., Pantis, J. D. & Sgardelis, S. P. (2008). How does habitat diversity affect the species–area relationship? *Global Ecology and Biogeography*, *17*(4), 532–538. https://doi.org/10.1111/j.1466-8238.2008.00393.x
Karlsson, A., Guillén, L. A. & Brukas, V. (2024). Regional forest green infrastructure planning and collaborative governance: A case study from southern Sweden. *Environmental Science & Policy*, *160*, 103840. https://doi.org/10.1016/j.envsci.2024.103840
Kershenbaum, A., Blumstein, D. T., Roch, M. A., Akçay, Ç., Backus, G., Bee, M. A., Bohn, K., Cao, Y., Carter, G., Cäsar, C., Coen, M., DeRuiter, S. L., Doyle, L., Edelman, S., Ferrer-i-Cancho, R., Freeberg, T. M., Garland, E. C., Gustison, M., Harley, H. E., . . . Zamora-Gutierrez, V. (2014). Acoustic sequences in non-human animals: a tutorial review and prospectus. *Biological Reviews/Biological Reviews of the Cambridge Philosophical Society*, *91*(1), 13–52. https://doi.org/10.1111/brv.12160
Kiester, A.R. (2013). Species Diversity, Overview. In S.A. Levin (Ed.), *Encyclopedia of Biodiversity* (2nd ed., pp. 706–714). Academic Press. https://doi.org/10.1016/B978-0-12-384719-5.00133-7
Komonen, A., & Kouki, J. (2008). Do restoration fellings in protected forests increase the risk of bark beetle damages in adjacent forests? A case study from Fennoscandian boreal forest. *Forest Ecology and Management*, *255*(11), 3736–3743. https://doi.org/10.1016/j.foreco.2008.03.029
Kouki, J., Hyvärinen, E., Lappalainen, H., Martikainen, P., & Similä, M. (2011). Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. *Diversity and Distributions*, *18*(4), 348–355. https://doi.org/10.1111/j.1472-4642.2011.00839.x
Kreutzweiser, D., Dutkiewicz, D., Capell, S., Sibley, P. & Scarr, T. (2020). Changes in streamside riparian forest canopy and leaf litter nutrient flux to soils during an emerald ash borer infestation in an agricultural landscape. *Biological Invasions*, *22*(6), 1865–1878. https://doi.org/10.1007/s10530-020-02223-7
Kupfer, J. A., Malanson, G. P. & Franklin, S. B. (2006). Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*, *15*(1), 8–20. https://doi.org/10.1111/j.1466-822x.2006.00204.x
Kuuluvainen, T. (2002). Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica*, *36*(1). https://doi.org/10.14214/sf.552
Laiolo, P. (2010). The emerging significance of bioacoustics in animal species conservation. *Biological Conservation*, *143*(7), 1635–1645. https://doi.org/10.1016/j.biocon.2010.03.025
Larrieu, L., Cabanettes, A., Gonin, P., Lachat, T., Paillet, Y., Winter, S., Bouget, C., & Deconchat, M. (2014). Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: A life-cycle approach to biodiversity monitoring. *Forest Ecology and Management*, *334*, 163–173. https://doi.org/10.1016/j.foreco.2014.09.007
Larson, A. J., Stover, K. C., & Keyes, C. R. (2012). Effects of restoration thinning on

spatial heterogeneity in mixed-conifer forest. *Canadian Journal of Forest Research*, *42*(8), 1505–1517. https://doi.org/10.1139/x2012-100
Lavorel, S., Díaz, S., Cornelissen, J. H. C., Garnier, E., Harrison, S. P., McIntyre, S., Pausas, J. G., Pérez-Harguindeguy, N., Roumet, C. & Urcelay, C. (2007). Plant functional types: Are we getting any closer to the Holy Grail? In *Springer eBooks* (pp. 149–164). https://doi.org/10.1007/978-3-540-32730-1_13
Leitao, P.J., Steffen, M. & Watt, A.D. (2018). Breeding bird species diversity across gradients of land use from forest to agriculture in Europe. *Ecography*, 41(8), 1331–1344. https://doi.org/10.1111/ecog.2018.v41.i810.1111/ecog.03295.
Lewinsohn, T. M. & Jorge, L. R. (2023). Species Diversity: Overview. In *Elsevier E Books* (pp. 275–286). https://doi.org/10.1016/b978-0-12-822562-2.00345-5
Lindbladh, M., & Bradshaw, R. (1998). The origin of present forest composition and pattern in southern Sweden. *Journal of Biogeography*, *25*(3), 463–477. https://doi.org/10.1046/j.1365-2699.1998.2530463.x
Loewen, C. J. G., Jackson, D. A. & Gilbert, B. (2022). Biodiversity patterns diverge along geographic temperature gradients. *Global Change Biology*, *29*(3), 603–617. https://doi.org/10.1111/gcb.16457
Loske, K. (1987b). Habitatwahl des Baumpiepers (Anthus trivialis). *Journal of Ornithology*, *128*(1), 33–47. https://doi.org/10.1007/bf01644789
Lubchenco, J. (1998). Entering the Century of the Environment: A new social contract for science. *Science*, *279*(5350), 491–497. https://doi.org/10.1126/science.279.5350.491
Magurran, E. (2004). *Measuring biological diversity*. Journal of Vegetation Science. Oxford, UK: Blackwell.15(6), 854-856. https://doi.org/10.1111/j.1654-1103.2004.tb02330.x
Massicotte, P., Frenette, J., Proulx, R., Pinel-Alloul, B., & Bertolo, A. (2013). Riverscape heterogeneity explains spatial variation in zooplankton functional evenness and biomass in a large river ecosystem. *Landscape Ecology*, *29*(1), 67–79. https://doi.org/10.1007/s10980-013-9946-1
Matthysen, E., Adriaensen, F., Dhondt, A. A., & Dhondt, A. A. (1995). Dispersal Distances of Nuthatches, Sitta europaea, in a Highly Fragmented Forest Habitat. *Oikos*, *72*(3), 375. https://doi.org/10.2307/3546123
Matthysen, E. & Adriaensen, F. (1998). Forest Size and Isolation Have No Effect on Reproductive Success of Eurasian Nuthatches (Sitta europaea). *Ornithology*, *115*(4), 955–963. https://doi.org/10.2307/4089513
McCain, C. M. (2005). Elevational gradients in diversity of small mammals *Ecology*, *86*(2), 366–372. https://doi.org/10.1890/03-3147
Metzger, F., & Schultz, J. (1984). Understory response to 50 years of management of a northern hardwood forest in Upper Michigan. *The American Midland Naturalist*, *112*(2), 209. https://doi.org/10.2307/2425428
Mikusinski, G., Roberge, J.-M. & Fuller, R. J. (Eds.). (2018). *Ecology and conservation of forest birds*. Cambridge University Press. Book.
Müller, J., & Bütler, R. (2010). A review of habitat thresholds for dead wood: a baseline f or management recommendations in European forests. *European Journal of Forest Research*, *129*(6), 981–992. https://doi.org/10.1007/s10342-010-0400-5
Munteanu, C., Kuemmerle, T., Keuler, N. S., Müller, D., Balázs, P., Dobosz, M., Griffiths, P., Halada, L., Kaim, D., Király, G., Konkoly-Gyuró, É., Kozak, J., Lieskovsky, J., Ostafin, K., Ostapowicz, K., Shandra, O., & Radeloff, V. C. (2015). Legacies of 19th century land use shape contemporary forest cover. *Global Environmental Change*, *34*, 83–94. https://doi.org/10.1016/j.gloenvcha.2015.06.015
Näslund, M. (1947). *Funktioner och tabeller för bestämning av avsmalning och formkvot under bark: Tall och gran i norra och södra Sverige* [Functions and tables for determining taper and form quotient under bark: Pine and spruce in northern and

southern Sweden]. Statens Skogsforskningsinstitut, Meddelanden nr 38(7). Stockholm: Forestry Research Institute of Sweden.
Niebuhr, B. B. S., Wosniack, M. E., Santos, M. C., Raposo, E. P., Viswanathan, G. M., Da Luz, M. G. E., & Pie, M. R. (2015). Survival in patchy landscapes: the interplay between dispersal, habitat loss and fragmentation. *Scientific Reports*, *5*(1). https://doi.org/10.1038/srep11898
Nikolov, S. C. (2008). Effect of stand age on bird communities in late-successional Macedonian pine forests in Bulgaria. *Forest Ecology and Management*, *257*(2), 580–587. https://doi.org/10.1016/j.foreco.2008.09.030
Öckinger, E., Schweiger, O., Crist, T. O., Debinski, D. M., Krauss, J., Kuussaari, M., Petersen, J. D., Pöyry, J., Settele, J., Summerville, K. S., & Bommarco, R. (2010). Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters*, *13*(8), 969–979. https://doi.org/10.1111/j.1461-0248.2010.01487.x
Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H. B. A., ... & Weedon, J. (2022). *vegan: Community Ecology Package (Version 2.6-2)* [R package]. https://www.researchgate.net/publication/360782912_vegan_community_ecology_package_version_26-2_April_2022
Olsson, J., Jonsson, B. G., Hjältén, J., & Ericson, L. (2011). Addition of coarse woody debris – The early fungal succession on Picea abies logs in managed forests and reserves. *Biological Conservation*, *144*(3), 1100–1110. https://doi.org/10.1016/j.biocon.2010.12.029
Östlund, L., Zackrisson, O., & Axelsson, A. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, *27*(8), 1198–1206. https://doi.org/10.1139/cjfr-27-8-1198
Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., & Gosselin, F. (2015). Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. *Forest Ecology and Management*, *346*, 51–64. https://doi.org/10.1016/j.foreco.2015.02.037
Pejchar, L., Pringle, R. M., Ranganathan, J., Zook, J. R., Duran, G., Oviedo, F. & Daily, G. C. (2008). Birds as agents of seed dispersal in a human-dominated landscape in southern Costa Rica. *Biological Conservation*, 141(2), 536–544. https://doi.org/10.1016/J.BIOCON.2007.11.008.
Pérez-Granados, C., & Traba, J. (2021). Estimating bird density using passive acoustic monitoring: a review of methods and suggestions for further research. *Ibis*, *163*(3), 765–783. https://doi.org/10.1111/ibi.12944
Piazzi, L., Gennaro, P., Cecchi, E., Bianchi, C., Cinti, M., Gatti, G., Guala, I., Morri, C., Sartoretto, F., Serena, F., & Montefalcone, M. (2020). Ecological status of coralligenous assemblages: Ten years of application of the ESCA index from local to wide scale validation. *Ecological Indicators*, *121*, 107077. https://doi.org/10.1016/j.ecolind.2020.107077
Porro, Z., Chiatante, G., & Bogliani, G. (2019). Associations between forest specialist birds and composition of woodland habitats in a highly modified landscape. *Forest Ecology and Management*, *458*, 117732. https://doi.org/10.1016/j.foreco.2019.117732
Rompré, G., Boucher, Y., Bélanger, L., Côté, S., & Robinson, W. D. (2010). Conserving biodiversity in managed forest landscapes: The use of critical thresholds for habitat. *The Forestry Chronicle*, *86*(5), 589–596. https://doi.org/10.5558/tfc86589-5
Rondeux, J., & Sanchez, C. (2009). Review of indicators and field methods for monitoring

biodiversity within national forest inventories. Core variable: Deadwood. Environmental Monitoring and Assessment, 164(1–4), 617–630. https://doi.org/10.1007/s10661-009-0917-6

Ross, S. R. P., O'Connell, D. P., Deichmann, J. L., Desjonquères, C., Gasc, A., Phillips, J. N., Sethi, S. S., Wood, C. M., & Burivalova, Z. (2023). Passive acoustic monitoring provides a fresh perspective on fundamental ecological questions. *Functional Ecology*, *37*(4), 959–975. https://doi.org/10.1111/1365-2435.14275

Sand-Jensen, K. (2001). Freshwater Ecosystems, Human Impact on. In S.A. Levin (Ed.), Encyclopedia of Biodiversity (pp. 89-108). Academic Press. https://doi.org/10.1016/B0-12-226865-2/00131-0.

Sattler, T., Pezzatti, G. B., Nobis, M. P., Obrist, M. K., Roth, T., & Moretti, M. (2013). Selection of multiple umbrella species for functional and taxonomic diversity to represent urban biodiversity. *Conservation Biology*, *28*(2), 414–426. https://doi.org/10.1111/cobi.12213

Severns, P. M., & Sykes, E. M. (2020). Indicator Species Analysis: a useful tool for plant disease studies. Phytopathology, 110(12), 1860–1862. https://doi.org/10.1094/phyto-12-19-0462-le

Shaw, T., Hedes, R., Sandstrom, A., Ruete, A., Hiron, M., Hedblom, M., Eggers, S., & Mikusiński, G. (2021). Hybrid bioacoustic and ecoacoustic analyses provide new links between bird assemblages and habitat quality in a winter boreal forest. *Environmental and Sustainability Indicators*, 11, 100141. https://doi.org/10.1016/j.indic.2021.100141.

Shipley, A. A., Murphy, M. T., & Elzinga, A. H. (2013). Residential edges as ecological traps: Postfledging survival of ground-nesting passerine in a forested urban park. *Ornithology*, *130*(3), 501–511. https://doi.org/10.1525/auk.2013.12139

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. *Ecological Bulletins*, *49*, 11–41. https://www.jstor.org/stable/20113262

Society for Ecological Restoration (SER), (2004). The SER international primer on ecological restoration. Science and Policy Working Group.

Spies, T. A., Hemstrom, M. A., Youngblood, A., & Hummel, S. (2006). Conserving Old-Growth forest diversity in Disturbance-Prone landscapes. *Conservation Biology*, *20*(2), 351–362. https://doi.org/10.1111/j.1523-1739.2006.00389.x

Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., De Vries, W., De Wit, C.A. & Folke, C. (2015). Planetary boundaries: Guiding human development on a changing planet. Science, 347(6223). https://doi.org/10.1126/science.1259855

Storch, F., Dormann, C. F., & Bauhus, J. (2018). Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring. *Forest Ecosystems*, *5*(1). https://doi.org/10.1186/s40663-018-0151-1

Sueur, J., Farina, A., Gasc, A., Pieretti, N., & Pavoine, S. (2014). Acoustic indices for biodiversity assessment and landscape investigation. *Acta Acustica United With Acustica*, *100*(4), 772–781. https://doi.org/10.3813/aaa.918757

Sugai, L. S. M., Silva, T. S. F., Ribeiro, J. W. & Llusia, D. (2018). Terrestrial Passive Acoustic Monitoring: Review and Perspectives. *BioScience*, *69*(1), 15–25. https://doi.org/10.1093/biosci/biy147

Sveaskog (2005). Management plan over Ecopark Käringberget. Sveaskog website. https://www.sveaskog.se/globalassets/jakt-fiske-och-friluftsliv/ekoparker/ekoparksplan-karingberget-3_060307.pdf

Sveaskog (2008). Management plan over Ecopark Hornsö. Sveaskog website. https://www.sveaskog.se/globalassets/jakt-fiske-och-friluftsliv/ekoparker/ekoparksplanhornso.pdf

Sveaskog (No date). Våra ekoparker. Sveaskog website.

https://www.sveaskog.se/vart-skogsbruk/skog-med-hoga-naturvarden/vara-ekoparker/
Swedish Forest Agency. (2022). Sustainable forests: In-depth evaluation 2023. (Report 2022-12). https://www.skogsstyrelsen.se/globalassets/om-oss/rapporter/rapporter-20222021202020192018/rapport-2022-12-sustainable-forests-in-depth-evaluation-2023-english-summary.pdf
Sykes, M. T., Prentice, I. C., & Cramer, W. (1996). A Bioclimatic Model for the Potential Distributions of North European Tree Species Under Present and Future Climates. *Journal of Biogeography, 23*(2), 203–233.
Tappeiner, J. C., II, & Alaback, P. B. (1989). Early establishment and vegetative growth of understory species in the western hemlock – Sitka spruce forests of southeast Alaska. *Canadian Journal of Botany*, *67*(2), 318–326. https://doi.org/10.1139/b89-046
Terborgh, J. (1977). Bird species diversity on an andean elevational gradient. *Ecology*, *58*(5), 1007–1019. https://doi.org/10.2307/1936921
Thomas, J.W., Anderson, R.G., Maser, C. & Bull, E.L., (1979). Wildlife habitats inmanaged forests of the Blue Mountains of Oregon and Washington. UnitedStates Department of Agriculture, Forest Service, Agricultural Handbook, p. 553.
Tranberg, O., Hekkala, A., Lindroos, O., Löfroth, T., Jönsson, M., Sjögren, J., & Hjältén, J. (2024). Translocation of deadwood in ecological compensation: A novel way to compensate for habitat loss. *AMBIO*, *53*(3), 482–496. https://doi.org/10.1007/s13280-023-01934-0
Trumbore, S., Brando, P., & Hartmann, H. (2015). Forest health and global change. Science, 349(6250), 814–818. https://doi.org/10.1126/science.aac6759
Uezu, A., & Metzger, J. P. (2011). Vanishing bird species in the Atlantic Forest: relative importance of landscape configuration, forest structure and species characteristics. *Biodiversity and Conservation*, *20*(14), 3627–3643. https://doi.org/10.1007/s10531-011-0154-5
Valerio, F., Basile, M., Balestrieri, R., Posillico, M., Di Donato, S., Altea, T., & Matteucci, G. (2016). The reliability of a composite biodiversity indicator in predicting bird species richness at different spatial scales. *Ecological Indicators*, *71*, 627–635. https://doi.org/10.1016/j.ecolind.2016.07.043
Van Der Plas, F., Manning, P., Soliveres, S., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., . . . Fischer, M. (2016). Correction for van der Plas et al., Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences*, *113*(18). https://doi.org/10.1073/pnas.1605668113
Versluijs, M., Hekkala, A.-M., Lindberg, E., Lämås, T., & Hjältén, J. (2020). Comparing the effects of even-aged thinning and selective felling on boreal forest birds. *Forest Ecology and Management, 475*, 118404. https://doi.org/10.1016/j.foreco.2020.118404
Wallenius, T., Niskanen, L., Virtanen, T., Hottola, J., Brumelis, G., Angervuori, A., Julkunen, J., & Pihlström, M. (2010). Loss of habitats, naturalness and species diversity in Eurasian forest landscapes. *Ecological Indicators*, *10*(6), 1093–1101. https://doi.org/10.1016/j.ecolind.2010.03.006
Warton, D. I., Lyons, M., Stoklosa, J., & Ives, A. R. (2016). Three points to consider when choosing a LM or GLM test for count data. *Methods in Ecology and Evolution*, *7*(8), 882–890. https://doi.org/10.1111/2041-210x.12552
Wesołowski, T. (2005). Virtual Conservation: How the European Union is Turning a Blind Eye to Its Vanishing Primeval Forests. *Conservation Biology*, *19*(5), 1349–1358. https://doi.org/10.1111/j.1523-1739.2005.00265.x
Whelan, C. J., & Maina, G. G. (2005). Effects of season, understorey vegetation density,

habitat edge and tree diameter on patch-use by bark-foraging birds. *Functional Ecology*, *19*(3), 529–536. https://doi.org/10.1111/j.1365-2435.2005.00996.x

Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, *28*(4), 453–470. https://doi.org/10.1046/j.1365-2699.2001.00563.x

Wilson, K. A., Lulow, M., Burger, J., Fang, Y., Andersen, C., Olson, D., O'Connell, M., & McBride, M. F. (2011). Optimal restoration: accounting for space, time and uncertainty. *Journal of Applied Ecology*, *48*(3), 715–725. https://doi.org/10.1111/j.1365-2664.2011.01975.x

Winiarska, D., Szymański, P., & Osiejuk, T. S. (2024). Detection ranges of forest bird vocalisations: guidelines for passive acoustic monitoring. Scientific Reports, 14(1). https://doi.org/10.1038/s41598-024-51297-z

Appendix 1. Sampling design in Käringberget Ecopark (2024)

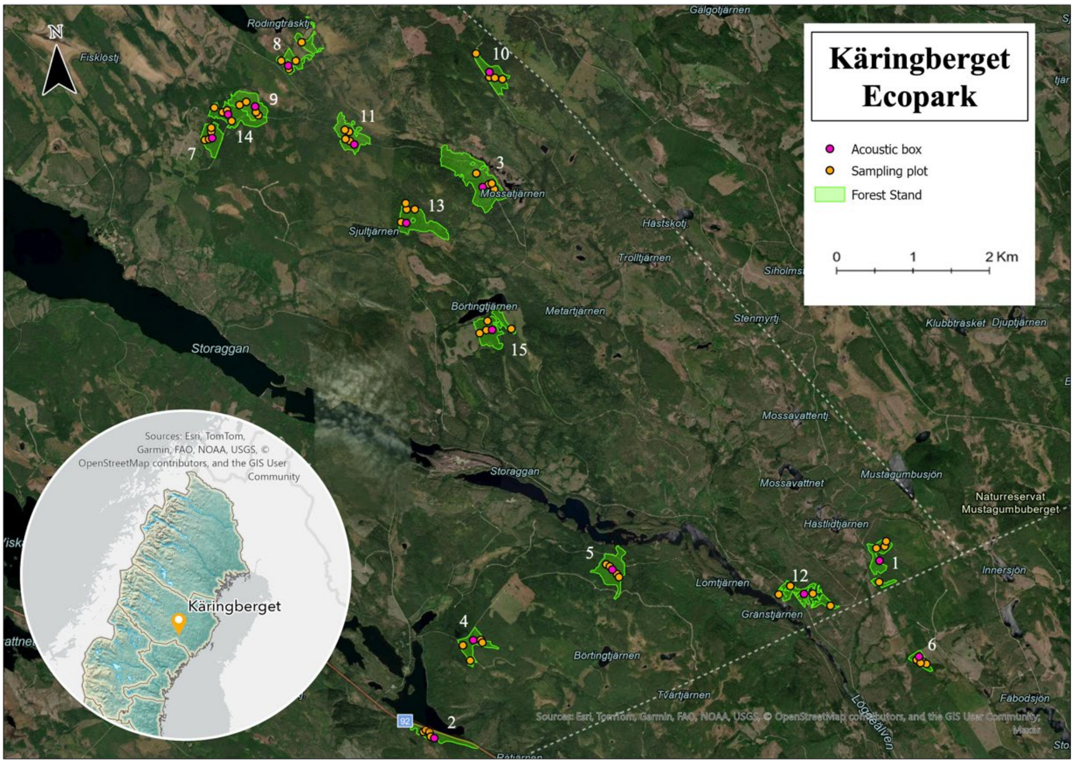


Figure 11: Sampling design in Käringbergt Ecopark (2024), showing the distribution of random sampling plots (orange dots) and the placement of the acoustic box (pink dot). Forest stand boundaries and locations are shown in green. Treatment classifications include: target stands – 3, 6, 10, 11, 15; restored stand - 4, 7, 8, 13, 14; unrestored stand – 1, 2, 5, 9, 12.

Appendix 2. Calculation formulas for deadwood volumes for coniferous and broadleaved trees

Volume formula for conifers (Pine & Spruce)
$(V_c) = 0.09314 * D^2 + 0.03069 * D^2 * H + 0.002818 * D * H^2$

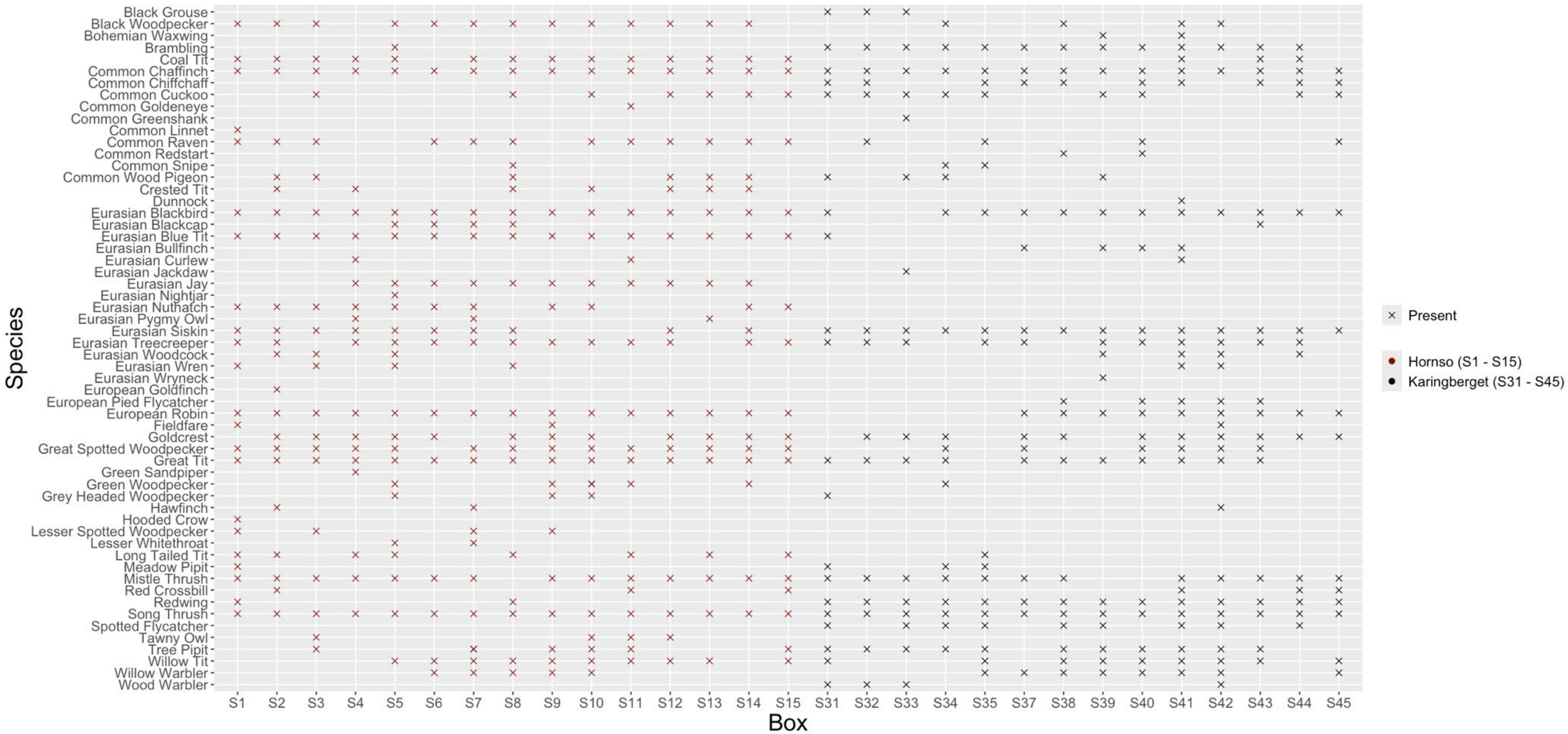
Volume formula for broadleaves (Alder & Ash & Aspen & Beech & Birch & Hazel & Lime & Oak & Rowan & Salix)
$(V_b) = 0.03715 * D^2 + 0.02892 * D^2 * H + 0.004983 * D * H^2$

Volume formula to calculate logs
$(V_t) = \frac{1}{3} * \pi * L (r_{max}^2 + r_{max} * r_{min} + r_{min}^2)$

D = Diameter at breast height
H = Height
V = Volume
L = length
r_{max} = maximum radius
r_{min} = minimum radius

Appendix 3. List of bird species detected in each acoustic box

Table 3: List of all bird species detected per acoustic box in Hornsö (red closs, left) and Käringberget (black cross, right). Box labels are indicated below.



Appendix 4. List of excluded non-forest bird species

The following species were excluded from the analysis due to their weak association with forest habitats:

- Barnacle Goose (*Branta leucopsis*)
- Black-headed Gull (*Chroicocephalus ridibundus*)
- Common Buzzard (*Buteo buteo*) – Excluded due to uncertain habitat association
- Common Gull (*Larus canus*)
- Common Crane (*Grus grus*)
- Eurasian Coot (*Fulica atra*)
- Greylag Goose (*Anser anser*)
- Mallard (*Anas platyrhynchos*)
- Red-throated Loon (*Gavia stellata*),
- Whooper Swan (*Cygnus cygnus*)

Non-forest bird specialists retained in the dataset due to their association with forests during the nesting period, as they may nest in or utilize tree habitats:

- Common Snipe (*Gallinago gallinago*)
- Common Goldeneye (*Bucephala clangula*)
- Greenshank (*Tringa nebularia*)
- Curlew (*Numenius arquata*)
- Sandpiper species (*Actitis hypoleucos*)

Appendix 5. Functional group classification.

Appendix 5. Functional group classification

Table 4: Overview of functional traits assigned to bird species detected in the study, including IUCN red-listed status, foraging strategy, nesting behaviour, and habitat preferences.

Common Name	Scientific Name	Red-listed	Foraging Type	Nesting Type	Habitat Type
Barnacle Goose	Branta leucopsis	Yes	Ground-feeders	Mountain cliffs	Wetland
Black Grouse	Tetrao tetrix	Yes	Ground-feeders	Ground	Mixed / Young forest
Black Headed Gull	Chroicocephalus ridibundus	No	Opportunistic	Ground	Wetland
Black Woodpecker	Dryocopus martius	No	Bark-feeders	Cavity	Mature forest
Boheimian Waxwing	Bombycilla garrulus	Yes	Crown-feeders	Off ground	Generalist
Brambling	Fringilla montifringilla	No	Crown /Ground- feeders	Off ground	Generalist
Coal Tit	Periparus ater	No	Crown-feeders	Cavity	Mature forest
Common Buzzard	Buteo buteo	No	Predator	Off ground	Generalist
Common Chaffinch	Fringilla coelebs	No	Crown /Ground- feeders	Off ground	Generalist
Common Chiffchaff	Phylloscopus collybita	No	Crown-feeders	Ground	Mature forest
Common Crane	Grus grus	Yes	Ground-feeders	Ground	Wetland
Common Cuckoo	Cuculus canorus	Yes	Crown-feeders	Parasite	Generalist
Common Goldeneye	Bucephala clangula	No	Wetland-feeders	Ground	Wetland
Common Greenshank	Tringa nebularia	No	Wetland-feeders	Ground	Wetland
Common Gull	Larus canus	No	Opportunistic	Ground	Wetland
Common Linnet	Carduelis cannabina	No	Crown-feeders	Off ground	Generalist

Common Raven	Corvus corax	No	Opportunistic	Off ground	Generalist
Common Redstart	Phoenicurus phoenicurus	Yes	Crown-feeders	Cavity	Mature forest
Common Snipe	Gallinago gallinago	No	Wetland-feeders	Ground	Wetland
Common Wood Pigeon	Columba palumbus	No	Crown /Ground- feeders	Off ground	Mature forest
Crested Tit	Lophophanes cristatus	No	Crown-feeders	Cavity	Mature forest
Dunnock	Prunella modularis	No	Crown /Ground- feeders	Off ground	Mixed / Young forest
Eurasian Blackbird	Turdus merula	No	Ground-feeders	Off ground	Mixed / Young forest
Eurasian Blackcap	Sylvia atricapilla	No	Crown /Ground- feeders	Off ground	Mixed / Young forest
Eurasian Blue Tit	Cyanistes caeuleus	No	Crown-feeders	Cavity	Mature forest
Eurasian Bullfinch	Pyrrhula pyrrhula	No	Crown-feeders	Off ground	Mature forest
Eurasian Coot	Fulica atra	No	Wetland-feeders	Ground	Wetland
Eurasian Curlew	Numenius arquata	Yes	Ground-feeders	Ground	Wetland
Eurasian Jackdaw	Corvus monedula	No	Opportunistic	Off ground	Generalist
Eurasian Jay	Garrulus glandarius	Yes	Crown /Ground- feeders	Off ground	Generalist
Eurasian Nightjar	Caprimulgus europaeus	Yes	Ground-feeders	Ground	Generalist
Eurasian Nuthatch	Sitta europaea	No	Bark-feeders	Cavity	Mature forest

Eurasian Pygmy Owl	Glaucidium passerinum	Yes	Predator	Cavity	Generalist
Eurasian Siskin	Spinus spinus	Yes	Crown-feeders	Off ground	Mature forest
Eurasian Treecreeper	Certhia familiaris	No	Bark-feeders	Cavity	Mature forest
Eurasian Woodcock	Scolopax rusticola	No	Ground-feeders	Ground	Mixed / Young forest
Eurasian Wren	Troglodytes troglodytes	No	Ground-feeders	Ground	Mature forest
Eurasian Wryneck	Jynx torquilla	Yes	Bark-feeders	Cavity	Mixed / Young forest
European Goldfinch	Carduelis carduelis	No	Crown-feeders	Off ground	Mixed / Young forest
European Pied Flycatcher	Ficedula hypoleuca	Yes	Crown-feeders	Cavity	Mature forest
European Robin	Erithacus rubecula	Yes	Ground-feeders	Off ground	Generalist
Fieldfare	Turdus pilaris	No	Ground-feeders	Off ground	Mixed / Young forest
Goldcrest	Regulus regulus	Yes	Crown-feeders	Off ground	Mature forest
Graylag Goose	Anser anser	No	Ground-feeders	Ground	Wetland
Great Spotted Woodpecker	Dendrocopos major	Yes	Bark-feeders	Cavity	Generalist
Great Tit	Parus major	Yes	Crown-feeders	Cavity	Generalist
Green Sandpiper	Tringa ochropus	No	Ground-feeders	Ground	Wetland

Green Woodpecker	Picus viridis	Yes	Bark-feeders	Cavity	Mature forest
Grey Headed Woodpecker	Picus canus	Yes	Bark-feeders	Cavity	Mature forest
Hawfinch	Coccothraustes coccothraustes	No	Crown-feeders	Off ground	Mature forest
Hooded Crow	Corvus cornix	No	Opportunistic	Off ground	Generalist
Lesser Spotted Woodpecker	Dryobates minor	Yes	Bark-feeders	Cavity	Mature forest
Lesser Whitethroat	Sylvia curruca	No	Ground-feeders	Ground	Mixed / Young forest
Long Tailed Tit	Aegithalos caudatus	No	Bark-feeders	Cavity	Generalist
Mallard	Anas platyrhynchos	No	Wetland-feeders	Ground	Wetland
Meadow Pipit	Anthus pratensis	Yes	Ground-feeders	Ground	Mixed / Young forest
Mistle Trush	Turdus viscivorus	Yes	Ground-feeders	Off ground	Mature forest
Red Crossbill	Loxia curvirostra	No	Crown-feeders	Off ground	Mature forest
Red Throated Loon	Gavia stellata	No	Wetland-feeders	Ground	Wetland
Redwing	Turdus illiacus	Yes	Ground-feeders	Off ground	Mixed / Young forest
Song Thrush	Turdus philomelos	Yes	Ground-feeders	Off ground	Mature forest
Spotted Flycatcher	Muscicapa striata	Yes	Crown-feeders	Cavity	Mature forest
Tawny Owl	Strix aluco	Yes	Predator	Cavity	Mature forest

Tree Pipit	Anthus trivialis	No	Ground-feeders	Ground	Generalist
Whooper Swan	Cygnus cygnus	No	Wetland-feeders	Ground	Wetland
Willow Tit	Poecile montanus	No	Crown-feeders	Cavity	Mature forest
Willow Warbler	Phylloscopus trochilus	No	Crown-feeders	Ground	Mature forest
Wood Warbler	Phylloscopus sibilatrix	No	Crown-feeders	Ground	Mature forest
			Crown /Ground-feeders = flexible feeders, Opportunistic = everywhere and anything they find, Wetland = around and in water food, Predator = predation food	Off-ground = Tree- or shrub-nesting	

Appendix 6. Deadwood volumes per stand in each study area

Figure 12: Deadwood volume (m^3/ha) across forest stands within Hornsö Ecopark. Each bar represents the total deadwood volume of a single stand, average across plots. Treatments are categorized to illustrate variation in deadwood volumes among stand.

Figure 13: Deadwood volume (m^3/ha) across forest stands within Käringberget Ecopark. Each bar represents the total deadwood volume of a single stand, average across plots. Treatments are categorized to illustrate variation in deadwood volumes among stand.

Appendix 7. Tree species composition (basal area) per stand in each study area

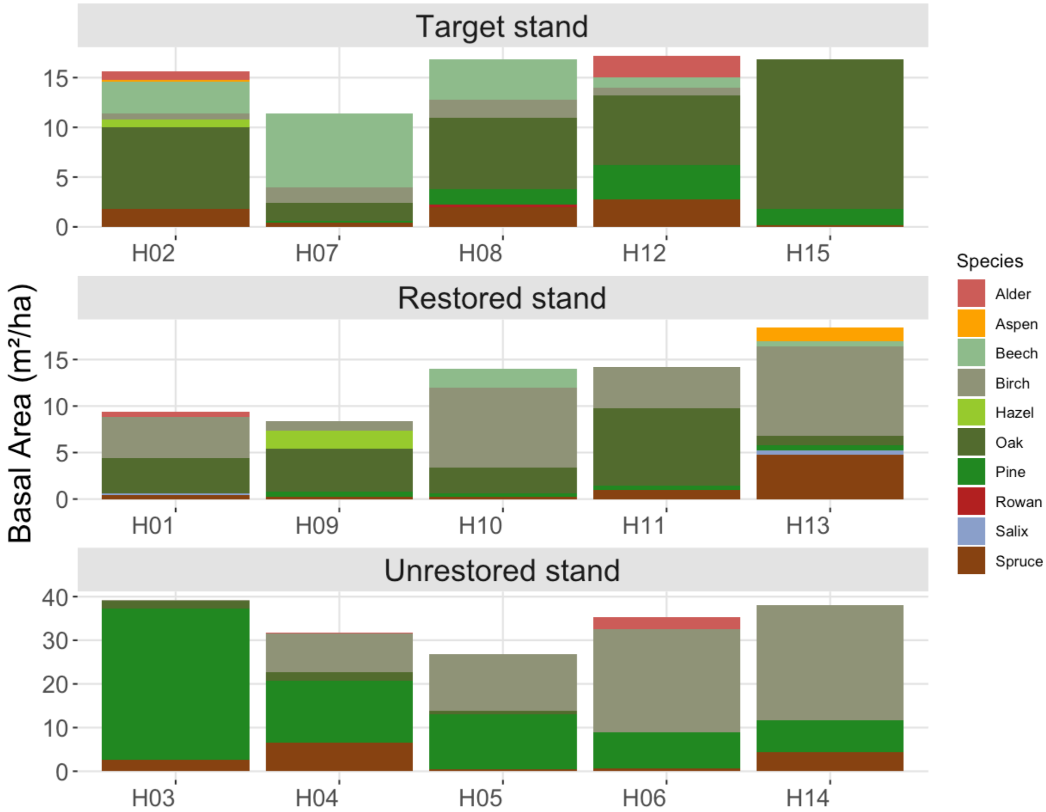


Figure 14: Basal area (m^2/ha) per tree species across forest stands within Hornsö Ecopark. Each bar represents the total basal area of a single stand, average across plots, with colors showing the contribution of each tree species. Treatments are categorized to illustrate variation in species dominance among stand.

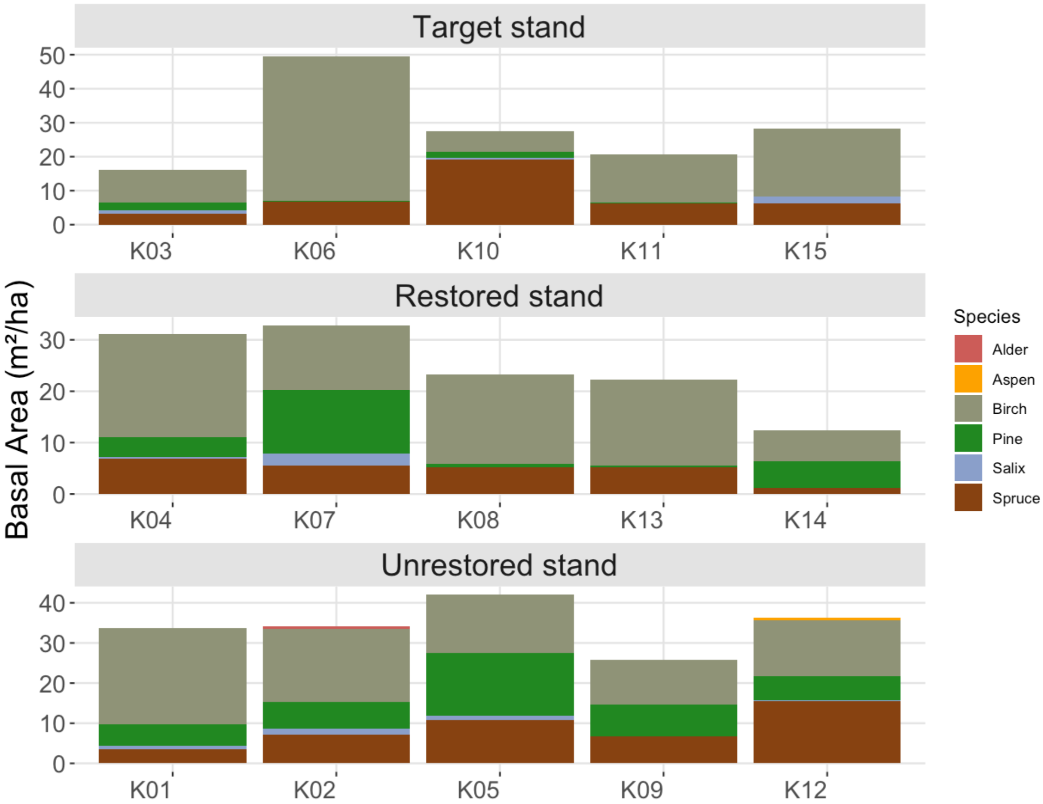


Figure 15: Basal area (m^2/ha) per tree species across forest stands within Käringberget Ecopark. Each bar represents the total basal area of a single stand, average across plots, with colors showing the contribution of each tree species. Treatments are categorized to illustrate variation in species dominance among stand.

Appendix 8. Understory composition (basal area) per stand in each study area

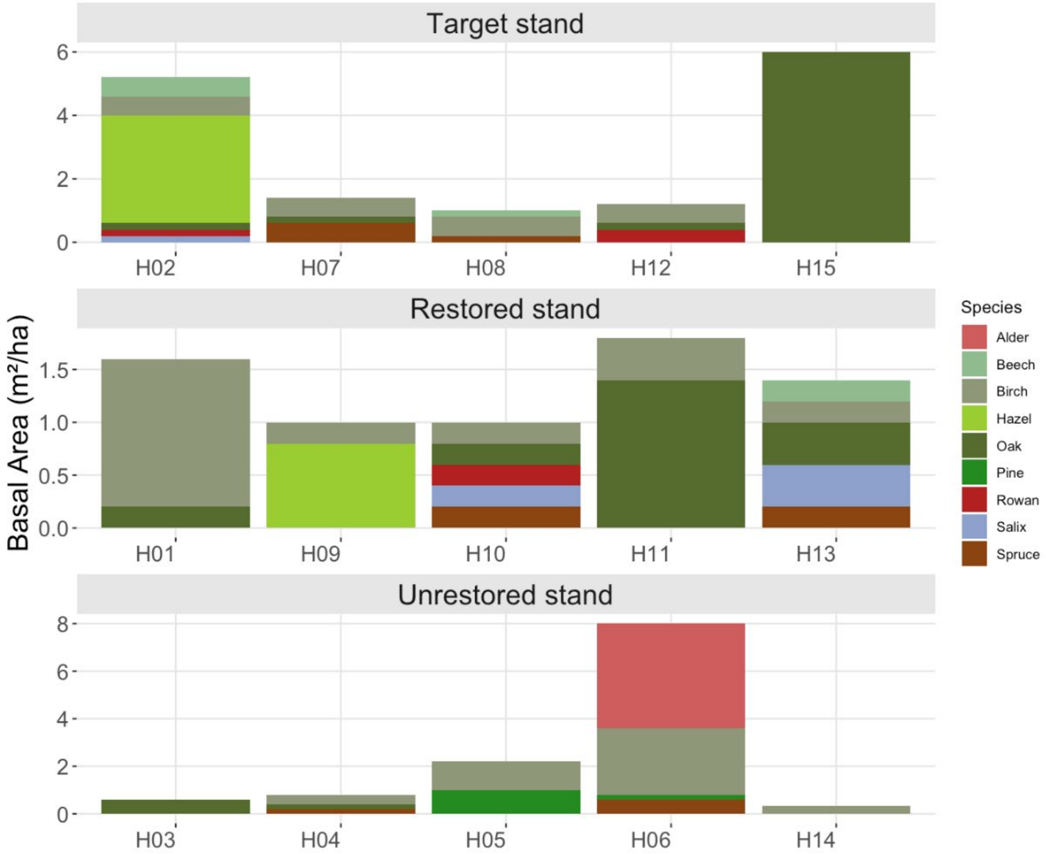


Figure 16: Basal area (m^2/ha) of understory cover across forest stands within Hornsö Ecopark. Each bar represents the total basal area of a single stand, average across plots, with colors showing the contribution of each tree species. Treatments are categorized to illustrate variation in species dominance within the understory layer among stand.

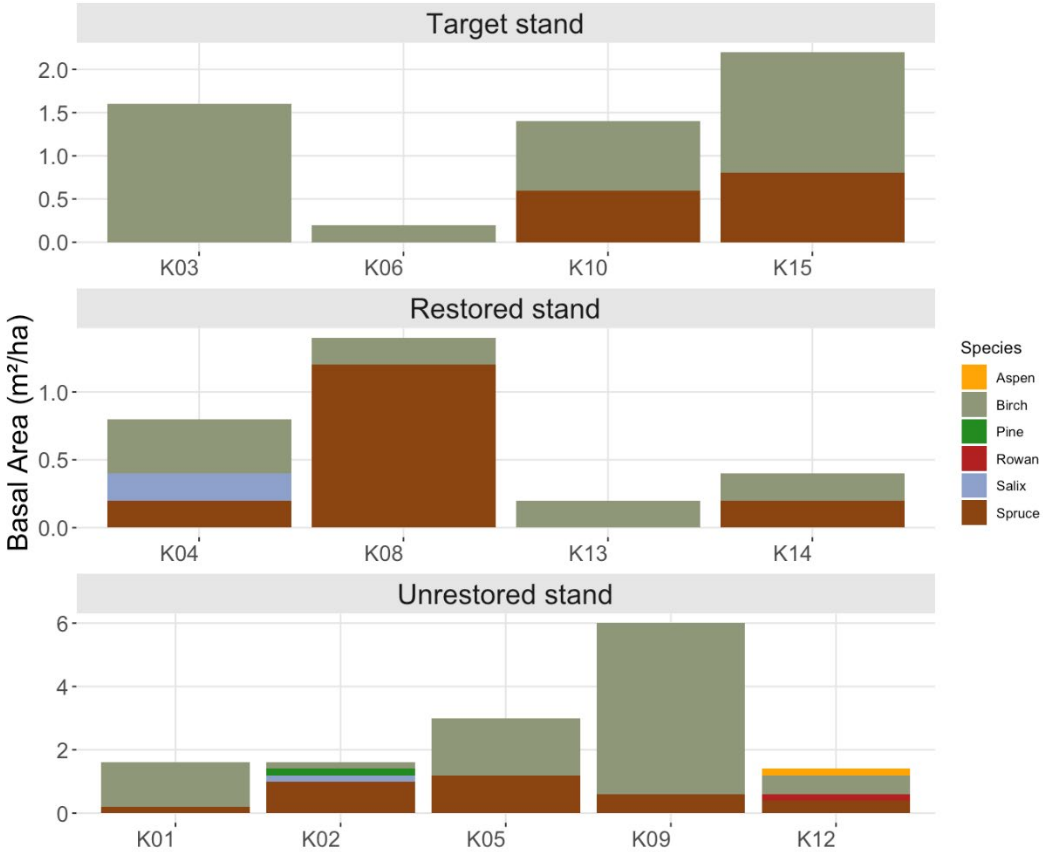


Figure 17: Basal area (m^2/ha) of understory cover across forest stands within Käringberget Ecopark. Each bar represents the total basal area of a single stand, average across plots, with colors showing the contribution of each tree species. Treatments are categorized to illustrate variation in species dominance within the understory layer among stand. Missing stands K07 and K11 are due to the absence of understory cover in those areas.

Appendix 9. Results of the functional groups analysis conducted in Hornsö

Table 5: Pairwise comparisons of bird species richness between functional groups in Hornsö, based on Wilconxon rank-sum tests. An asterisk (*) indicates a statistically significant difference (p < 0.05).

	Cavity	Ground	Off ground	Bark feeders	Crown feeders	Ground feeders	Flexible feeders	Generalist	Mature forest
Ground	**0.0007***								
Off ground	1	**0.0008***							
Bark feeders	**0.0002***	**0.0045***	**0.0001***						
Crown feeders	**0.0081***	**0.0008***	**0.0029***	**0.0288***					
Ground feeders	**0.0004***	**0.0013***	**0.0003***	1	0.2712				
Flexible feeders	**0.0001***	**0.0369***	**0.0001***	1	**0.0003***	0.1718			
Generalist	**0.0105***	**0.0007***	**0.0063***	**0.0024***	1	**0.0332***	**0.0002***		
Mature forest	0.0981	**0.0008***	0.2379	**0.0001***	**0.0002***	**0.0001***	**0.0001***	**0.0002***	
Young mixed forest	**0.0001***	1	**0.0001***	**0.0018***	**0.0001***	**0.0003***	**0.0207***	**0.0001***	**0.0001***

Table 6: Table includes the mean, median, and standard deviation (SD) of bird species richness for each fucntional group in Hornsö.

Guild	Mean	Median	SD	n
Mature forest	11.3	12	1.68	15
Off ground	9.47	10	1.30	15
Cavity	9.27	9	1.44	15
Generalist	7.33	8	1.05	15
Crown feeders	6.8	7	1.26	15
Bark feeders	4.73	5	1.33	15
Ground feeders	5.33	5	1.40	15
Flexible feeders	3.8	4	1.01	15
Ground	2	2	1	11
Young Mixed Forest	2	2	1.13	15

Table 7: Differences between treatments within a functional group (Hornsö Ecopark). Kruskal-wallis test to assess differences among treatments, followed by pairwise post-hoc Dunn's tests. $X^2(2)$ = Kruskal-Wallis chi-square value with 2 degrees of freedom, T = target stand, R = restored stand, U = Unrestored stand, p = p-value (significant at $p < 0.05$).*

Functional group		Kruskal-Wallis	Post-hoc Dunn's Test	Mean
Nesting	Cavity	$X^2(2) = 1.917$, p = 0.384		
	Ground	$X^2(2) = 0.614$, p = 0.736		
	Off-ground	$X^2(2) = 2.210$, p = 0.331		
Foraging	Bark	$X^2(2) = 6.203$, **p = 0.045***	T - R: $X^2 = 1.557$; p = 0.179	T: 3.6
			R - U: $X^2 = 2.462$; **p = 0.021***	R: 3.8
			U - T: $X^2 = 0.905$; p = 0.548	U: 2.0
	Crown	$X^2(2) = 0.574$, p = 0.751		
	Ground	$X^2(2) = 3.654$, p = 0.161		
	Flexible	$X^2(2) = 2.784$, p = 0.249		
Habitat	Generalist	$X^2(2) = 1.658$, p = 0.436		
	Mature forest	$X^2(2) = 4.221$, p = 0.121		
	Young mixed forest	$X^2(2) = 2.647$, p = 0.266		

Appendix 10. Results of the functional groups analysis conducted in Käringberget

Table 8: Pairwise comparisons of bird species richness between functional groups in Käringberget, based on Wilconxon rank-sum tests. An asterisk (*) indicates a statistically significant difference (p < 0.05), while results with marginal significance (0.05 < p < 0.1) are indicated in with a dot (.).

	Cavity	Ground	Off ground	Bark feeders	Crown feeders	Ground feeders	Flexible feeders	Generalist	Mature forest
Ground	1								
Off ground	**0.0004***	**0.0003***							
Bark feeders	**0.0289***	0.2518	**0.0004***						
Crown feeders	*0.0581.*	**0.0004***	0.1373	**0.0004***					
Ground feeders	1	**0.0011***	**0.0009***	**0.0004***	0.7524				
Flexible feeders	0.3154	1	**0.0002***	0.5075	**0.0002***	**0.0002***			
Generalist	1	**0.0033***	**0.0004***	**0.0004***	0.3656	1	**0.0003***		
Mature forest	**0.0007***	**0.0003***	1	**0.0004***	0.8266	**0.0032***	**0.0002***	**0.0007***	
Young mixed forest	0.6237	1	**0.0003***	0.5661	**0.0003***	**0.0002***	1	**0.0006***	**0.0003***

Table 9: Table includes the mean, median, and standard deviation (SD) of bird species richness for each functional group in Käringberget.

Guild	Mean	Median	SD	n
Off ground	9.64	10	1.34	14
Mature forest	9.5	8.5	2.28	14
Crown feeders	7.75	7	1.91	14
Ground feeders	6.07	6	1.21	14
Generalist	5.79	6	1.12	14
Cavity	4.64	5	2.02	14
Ground	3.21	3	1.19	14
Young Mixed Forest	2.86	3	0.86	14
Flexible feeders	2.71	3	0.61	14
Bark feeders	1.92	2	0.76	13

Table 10: Differences between treatments within a functional group (Käringberget Ecopark). Kruskal-wallis test to assess differences among treatments, followed by pairwise post-hoc Dunn's tests. $X^2(2)$ = Kruskal-Wallis chi-square value with 2 degrees of freedom, T = target stand, R = restored stand, U = Unrestored stand, p = p-value (significant at $p < 0.05$), while results with marginal significance ($0.05 < p < 0.1$) are indicated with a dot (.).*

Functional group		Kruskal-Wallis	Post-hoc Dunn's Test	Mean
Nesting	Cavity	$X^2(2) = 2.814$, p = 0.245		
	Ground	$X^2(2) = 7.026$, **p = 0.029***	T - R: $X^2 = 0.079$; p = 1	T: 3.6
			R - U: $X^2 = 2.374$; **p = 0.026***	R: 3.8
			U - T: $X^2 = 2.300$; **p = 0.032***	U: 2.0
	Off-ground	$X^2(2) = 2.480$, p = 0.289		
Foraging	Bark	$X^2(2) = 1.092$, p = 0.579		
	Crown	$X^2(2) = 0.877$, p = 0.645		
	Ground	$X^2(2) = 3.981$, p = 0.137		
	Flexible	$X^2(2) = 5.697$, *p = 0.058.*	T - R: $X^2 = 1.500$; p = 0.198	T: 3.20
			R - U: $X^2 = 1.567$; p = 0.534	R: 2.60
			U - T: $X^2 = 2.343$; **p = 0.029***	U: 2.25
Habitat	Generalist	$X^2(2) = 7.800$, **p = 0.020***	T - R: $X^2 = -1.783$; p = 0.112	T: 6.80
			R - U: $X^2 = 1.055$; p = 0.437	R: 5.60
			U - T: $X^2 = 2.736$; **p = 0.009***	U: 4.75
	Mature forest	$X^2(2) = 1.101$, p = 0.577		
	Young mixed forest	$X^2(2) = 1.469$, p = 0.480		

Appendix 11. Results of indicator species analysis (ISA) in each study area

Table 11: ISA for Hornsö Ecopark. Group codes: 1 = Target stand, 2 = Restored stand, 3 = Unrestored stand. Indval = Indicator Value; α- Specificity = probability that the species is exclusive to the group; β-Fidelity = frequency of occurrence within the group. An asterisk (*) indicates a statistically significant difference ($p < 0.05$), while results with marginal significance ($0.05 < p < 0.1$) are indicated in with a dot (.).

	Group	IndVal	P-value	α-Specificity	β-Fidelity
Tree Pipit	1	0.730	0.185		
Lesser Spotted Woodpecker	1	0.671	0.248		
Green Woodpecker	2	0.600	0.526		
Eurasian Curlew	3	0.632	0.290		
Eurasian Nuthatch	1 + 2	0.953	**0.012***	0.909	1
Crested Tit	2 + 3	0.837	*0.077.*		
Long Tailed Tit	2 + 3	0.783	0.301		
Common Wood Pigeon	2 + 3	0.645	0.811		

Table 12: ISA for Käringberget Ecopark. Group codes: 1 = Target stand, 2 = Restored stand, 3 = Unrestored stand. Indval = Indicator Value; α- Specificity = probability that the species is exclusive to the group; β-Fidelity = frequency of occurrence within the group. An asterisk (*) indicates a statistically significant difference ($p < 0.05$), while results with marginal significance ($0.05 < p < 0.1$) are indicated in with a dot (.).

	Group	IndVal	P-value	α-Specificity	β-Fidelity
Bohemian Waxwing	1	0.632	0.276		
Meadow Pipit	2	0.775	*0.071.*		
Black Woodpecker	2	0.671	0.163		
Common Snipe	2	0.632	0.289		
Tree Pipit	1 + 2	0.943	**0.013***	0.889	1
Spotted Flycatcher	1 + 2	0.832	0.135		
Common Wood Pigeon	1 + 2	0.632	0.447		
Wood Warbler	1 + 2	0.632	0.457		
Eurasian Wren	1 + 3	0.667	0.355		

Publishing and archiving

Approved students' theses at SLU can be published online. As a student you own the copyright to your work and in such cases, you need to approve the publication. In connection with your approval of publication, SLU will process your personal data (name) to make the work searchable on the internet. You can revoke your consent at any time by contacting the library.

Even if you choose not to publish the work or if you revoke your approval, the thesis will be archived digitally according to archive legislation.

You will find links to SLU's publication agreement and SLU's processing of personal data and your rights on this page:

- https://libanswers.slu.se/en/faq/228318

☒ YES, I/we have read and agree to the agreement for publication and the personal data processing that takes place in connection with this

☐ NO, I/we do not give my/our permission to publish the full text of this work. However, the work will be uploaded for archiving and the metadata and summary will be visible and searchable.