



Bird community response to even-aged and uneven-aged forest management in Mediterranean Scots pine forests

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Abstract

Understanding how biodiversity responds to forest management is a key challenge for sustainable forest management. Birds, as a sensitive taxon of habitat quality, provide valuable insights into the ecological consequences of different management types. In this study, we examined how even-aged (EA) and uneven-aged (UEA) management strategies, and their associated management stages influence bird communities in managed Scots pine (*Pinus sylvestris*) forests. We assessed species richness and abundance of forest specialists, generalists, and ecological guilds, and compared the relative explanatory power of management strategy, management stage, and forest structural attributes using data from 207 plots. UEA stands generally favoured forest specialists and forest generalists as well as cavity and understory nesters, and overstory and understory foragers. Bird communities varied among management stages: EA young stands showed the lowest values of forest specialists, cavity nesters and trunk and understory foragers, while UEA capitalized and EA preparatory cutting stages hosted the highest values of forest specialists and favoured cavity and overstory dependent guilds. Overall, management stage models better explained the variation in bird community than management strategy and structural variables models. We highlight that management stage played a decisive role in shaping avian communities. Ultimately, whether under EA or UEA systems, forest management should adopt a multifunctional approach that prioritizes biodiversity-relevant stages, enhances stand heterogeneity, and ensures the long-term conservation of forest biodiversity.

Keywords Forest management · Birds · Ecological guilds · Uneven-aged · Even-aged · Structural variables

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Introduction

Managing European forests is a topic under discussion, for which socioeconomic and ecological objectives must be pursued in synergy, while ensuring forests resilience and the provision of ecosystem services (European Commission 2021a). Historically, European forests have been intensely harvested and deforested for wood supply and land conversion to agriculture, with broad-scale impact on forest biodiversity (Bengtsson et al. 2000). In the last decade, forest protection has gained increasing attention within the framework of sustainable and multifunctional forest management promoted by the EU Forest Strategy for 2030 (European Commission 2021a). This strategy emphasizes both the protection of unmanaged old-growth forests and the application of biodiversity-oriented practices in managed forests, including deadwood retention, continuous forest cover, and uneven-aged silviculture.

Within this context of actively managed forests, conifer species such as Scots pine (*Pinus sylvestris*), have often

been favoured or reforested due to their productivity, management feasibility, economic interest, and broad ecological adaptability (Spiecker 2003; Pausas et al. 2004). Scots pine covers a widespread distribution range in Europe, extending from temperate and boreal zones to Mediterranean zone, where it is primarily found in mountainous areas ranging from approximately 700 m in elevation up to the upper montane zone. In recent decades, its distribution has expanded beyond its natural range in regions such as the Iberian Peninsula, primarily as a result of spontaneous natural regeneration favoured by forest owners (Mason and Alía 2000; Willoughby et al. 2008). This makes it one of the most important species for timber production in the Iberian Peninsula (Piqué et al. 2011).

Scots pine, like other pine species, can be managed under either even-aged (hereafter EA) or uneven-aged (hereafter UEA) forest management strategies in the Mediterranean region (Piqué et al. 2017; Beltrán et al. 2020). However, most Scots pine stands are managed as EA, especially on large public properties, due to its simpler management and higher timber production. This method characterized by successive and uniform thinning cycles every 10–30 years, is primarily implemented to maximize timber production (Nolet et al. 2018). These thinning cycles generate a sequence of management stages ranging from young stands, followed by preparatory and seedling cutting stands, and up to final felling stages, where regeneration restarts. As a result, stands maintain a consistent age structure over time and thus simplified and homogenised stand structures. On small private forestlands, the UEA forest management strategy has prevailed due to forestry tradition. This management strategy involves the selective removal of individual trees across a range of diameter classes, resulting in the development of UEA stand structures (Piqué et al. 2017; Nolet et al. 2018). These stands can adopt late-successional features that may better support ecological complexity and biodiversity (Kuuluvainen et al. 2012; Szmyt 2025). In this sense, there is growing consensus about prioritizing UEA forest management (Joelsson et al. 2017; Savilaakso et al. 2021) when integrating biodiversity objectives in forest management. Higher unevenness is thus considered a positive biodiversity indicator for forest ecosystems by the European Union (European Commission 2021a; Forest Europe 2026). Consequently, forest management strategy plays a crucial role in shaping structural attributes such as tree density, mean diameter, and canopy cover, factors that can significantly modulate the biodiversity that the forest can host (Zeller et al. 2023; Rigo et al. 2024; Komlós et al. 2024). However, in practical terms, it is important to identify whether management strategies per se or structural attributes better quantify biodiversity.

Forests managed under EA systems appear to sustain lower overall biodiversity (Kuuluvainen et al. 2012). However, as reviewed by (Nolet et al. 2018) empirical comparisons between these two silviculture approaches yield contrasting results, influenced by region, forest type, methodological differences, and studied taxa. Notably, most studies to date have been carried out in boreal forests where EA forest management usually ends up with a clear-cut where all trees are removed. Another approach of EA forest management is the shelterwood system, in which some trees are retained, allowing the maintenance (at least partially) of forest ecosystem conditions (Nyland 2010). In the Mediterranean context, EA forest management is usually applied following the shelterwood system, guaranteeing continuous cover forestry and natural regeneration acquisition until final felling, which may have different implications for biodiversity. Ultimately, biodiversity responses are shaped not only by the choice between even-aged and uneven-aged systems, but also by variation within these management strategies, including management stages and intensity (Nolet et al. 2018). Understanding whether these intermediate stages influence biodiversity – comparatively to overall EA and UEA strategies – remains essential to inform sustainable forest management in Mediterranean Scots pine forests.

Birds are a diverse taxon widely studied because they are sensitive to environmental changes (Canterbury et al. 2000; Gregory and Strien 2010) and particularly to management activities and forest structures (Gil-Tena et al. 2007; Ameztegui et al. 2018; Basile et al. 2021a). Because silvicultural treatments are typically applied at the stand level (management unit), they directly shape structural features that influence bird communities at that same spatial scale (Shaw et al. 2024; Rota et al. 2025). From a functional point of view, these structural variations may differently affect bird guilds, i.e. species that share similar habitat and resource needs and are therefore expected to respond similarly to forest management (Verner 1984; Balestrieri et al. 2015). For example, cavity nesters are particularly dependent on the presence of large-diameter trees and snags (Camprodon et al. 2008; Komlós et al. 2024). These structural elements, and consequently cavity availability, are often scarce in early management stages (Vuidot et al. 2011; Paillet et al. 2015), potentially limiting the suitability of these stands for cavity-nesting birds. On the other hand, bird species that use canopy as living environment, can be favoured in management stages with well-developed canopies, compared to final cutting stages where tree cover can be considerably reduced (Ameztegui et al. 2018).

Unlike most studies focused on Euro-Siberian forests (Schall et al. 2018; Versluijs et al. 2020), the present work aims to compare the effect of EA and UEA management strategies on bird communities in Scots pine forests within

a Mediterranean context, with a focus on ecological guilds. By integrating gradients of management intensity and forest developmental stages, we seek to move beyond simple binary comparisons and evaluate which factors have the more influence on bird communities: management strategies and their associated developmental stages – from a practical forest management perspective –, or forest structural attributes as more direct descriptors of forest conditions, which have already been reported to influence the bird community (Rigo et al. 2024; Komlós et al. 2024). To this end, we combined structural variables and management types with bird data from multiple Scots pine stands subjected to EA and UEA strategies in the northeastern Iberian Peninsula. Specifically, we address the following research questions: (i) Does the forest management strategy influence bird communities? (ii) Do bird guilds respond differently to the management stages conforming the EA and UEA strategies? (iii) Are bird communities more predicted by a management strategy, the management stages or by a set of forest structural variables?

We hypothesised that (i) UEA stands will support richer bird assemblages than EA stands and that, management stages will have more influence than the management strategy itself. We also hypothesised that (ii) bird guilds would respond differently along management stages, reflecting differences in their sensitivity to forest developmental stages and associated structural conditions. Specifically, we expected cavity nesters and trunk foragers to show higher abundances in UEA forests and in advanced stages of EA management, while overstory and understory nesters and foragers would respond primarily to variation in canopy and understory covers than to a management strategy/stage. Additionally, we predicted that (iii) forest structural variables, used as direct descriptors of stand conditions, would better explain the overall variation in bird community than management strategy or management stage categories commonly applied in forest planning.

Materials and methods

Study area and management types

This study was carried out in the montane zone of the eastern Pyrenees and Pre-Pyrenees of Catalonia (North-east of the Iberian Peninsula). We collected data from 207 plots located in native Scots pine (*Pinus sylvestris*) managed forests at elevations ranging from 700 m to 1880 m above the sea level. The forest composition is similar across all stands, which consists of pure Scots pine forests. The occurrence of deciduous trees in the codominant canopy layer is almost negligible, although deciduous species are represented in

the lower or subordinate tree layer. The main accompanying tree species are downy oak (*Quercus pubescens*) and beech (*Fagus sylvatica*). Where present, the shrub layer is dominated by common box (*Buxus sempervirens*), hazel (*Corylus avellana*), and hawthorn (*Crataegus monogyna*). Mean annual precipitation ranges from 650 to 1,000 mm and the mean May temperatures vary from 15 °C to 11 °C, according to the altitudinal gradient of the plots.

Stand was used as management unit, defined by a uniform forest structure, and serving as the spatial unit for management planning. Each stand had between one and four plots depending on stand size, and plots in the same stand were considered independent as they were separated with a minimum distance of 300 m. Stands were located throughout the distribution area of Scots pine in Catalonia, covering two bioclimatic regions that may differ in terms of bird communities: Nemoral and Oreoborealoide (Walter and Lieth 1960; Allue Andrade 1990). Due to forest ownership regimes, forests managed under UEA were mostly found in the Nemoral region (60 out of 71 plots) whereas EA forests were more equally distributed between both bioclimatic regions, with 56 plots in the Nemoral region and 80 in Oreoborealoide region (Fig. 1).

Studied stands (78) were managed following UEA (71 plots in 28 stands) and EA (136 plots in 50 stands) forest management strategies and subsequently classified into 6 different management stages depending on their development stage for EA stands and management intensity for UEA stands (Table 1). EA stands were managed using the uniform shelterwood system as regeneration technique, which implies regeneration cutting based on a series of progressive cuts that lead to the establishment of a new generation of seedlings before the seed trees are fully removed. Uniform shelterwood method has normally four phases: preparatory cutting, seedling cutting, removal cutting, and final cutting. However, depending on the different conditions of density and vitality of the trees that can be found prior the regeneration cut starts, the period where the regeneration cuts are implemented can be between 20 and 30 years and the phases can be reduced from four to three (Nyland 2010). EA stands were divided in four groups according to their age and its management stage.

- Young even-aged stands (E_You): forest stands with EA forest structure with a tree distribution comprising few diametric classes (Fig. A.1) and low structural diversity. They originated mainly by abandoned agricultural areas or pastures colonized by pines, currently 20–30 years old.
- Even-aged preparatory cuttings stands (E_Pre): forest stands with EA forest structure, comprising an intermediate stage of development, where thinning or

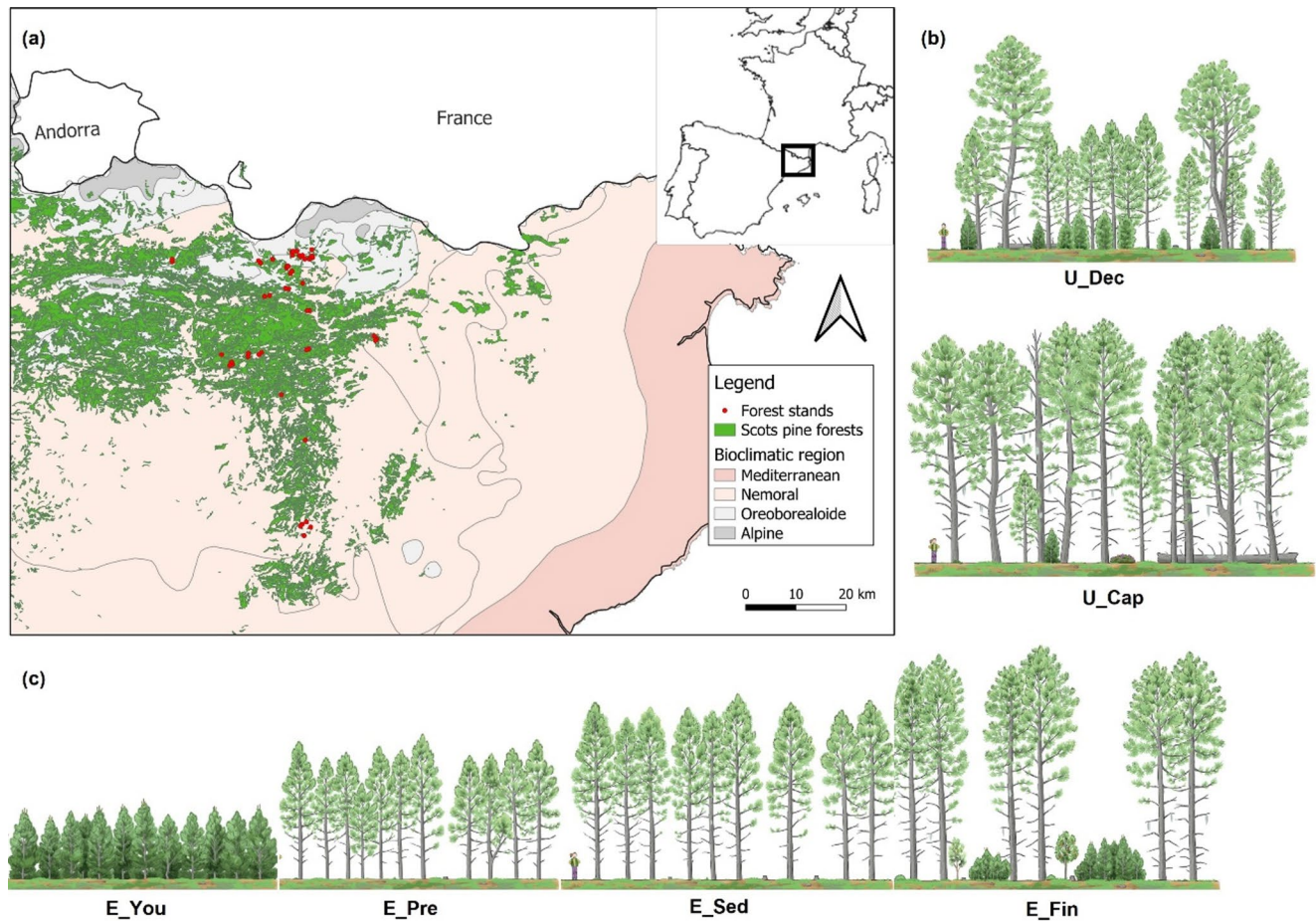


Fig. 1 **a** Study area in Catalonia (Northeastern of the Iberian Peninsula), with study sites location in red. **b** Uneven-aged management stages: U_Dec=UEA decapitalized stands; U_Cap=UEA capitalized stands. **c** Even-aged management stages: E_You=EA young stands;

E_Pre=EA preparatory cutting stands; E_Sed=EA seedling cutting stands; E_Fin=EA final felling stands. Each figure represents a theoretical overview of the management stages in our study context. Illustration design: Blanca Martí/ CTFC

Table 1 Number of studied plots, and mean value with standard deviation in brackets of the structural variables included in the models for each management strategy and management stage

Management	Code	Plots	GINI index	Dm (cm)	Ho (m)	N (tree/ha)	Und. cov. (%)	Can. cov. (%)
Management strategy	EA	136	0.17 (0.01)	21.78 (0.56)	14.74 (0.42)	616.41 (34.03)	26.59 (1.64)	39.68 (1.56)
	UEA	71	0.20 (0.01)	19.62 (0.72)	16.53 (0.54)	708.28 (39.49)	40.42 (1.88)	52.43 (1.80)
Management stage	E_You	26	0.11 (0.00)	13.21 (0.31)	6.78 (0.27)	845.56 (48.00)	15.19 (1.09)	42.50 (1.85)
	E_Pre	35	0.18 (0.01)	23.93 (0.69)	18.67 (0.52)	991.00 (58.09)	29.68 (3.70)	63.86 (1.91)
	E_Sed	26	0.15 (0.01)	22.62 (0.81)	16.83 (0.42)	476.02 (38.81)	32.73 (4.26)	30.77 (1.27)
	E_Fin	49	0.19 (0.01)	24.35 (0.99)	15.05 (0.44)	301.74 (36.46)	28.04 (2.63)	25.59 (1.30)
	U_Dec	31	0.17 (0.01)	14.92 (0.39)	12.43 (0.33)	855.89 (61.60)	38.75 (2.83)	50.49 (2.12)
	U_Cap	40	0.23 (0.01)	23.38 (0.89)	19.80 (0.50)	590.20 (45.77)	41.75 (2.52)	54.00 (2.73)

preparatory cuts have been carried out to initiate the regeneration. Canopy cover is still quite high (around 65%), with high tree density and some deadwood due to competition between stems. Stand age is approximately 55–70 years old, with some variability between stands due to the natural origin (± 10 –15 years).

- Even-aged seedling cuttings stands (E_Sed): forest stands with EA forest structure, comprising an adult development stage, where seedling cuttings have been implemented and canopy cover is around 30–35%. Stand age is around approximately 70–90 years old.

- Even-aged final felling stands (E_Fin): forest stands with EA forest structure where final cuttings have been implemented, retaining a percentage of trees to ensure natural regeneration and ecological characteristics. Canopy cover is around 20–25% with few scattered medium or large seed trees that can be up to 120 years old.

UEA forest management strategy is based on selective cutting applied in all tree sizes. The idea is to promote a mix of trees of different ages and sizes within the stands. In each intervention, all treatments described for EA stands are applied: thinning and regeneration cutting, since continuous cover and regeneration must be ensured. UEA stands typically have a reverse J-shaped diameter class distribution with a larger proportion of young trees, some medium trees, and few large trees (Baker 1996; Schütz 1997). UEA stands were divided in two situations:

- Decapitalized uneven-aged stands (U_Dec): forest stands with UEA structure having a high proportion of small-diameter trees. They often have only 3–5 diameter classes, with a clear predominance of the 10–15 and the 15–20 cm classes (fig. A.1) due to past high intensity harvesting and with trees ranging from 50 to 90 years old.
- Capitalized uneven-aged stands (U_Cap): forest stands with a more balanced UEA structure and having a higher proportion of larger trees due to moderate harvesting, which can be over 90–120 years old.

Bird surveys

Bird surveys were carried out in each of the 207 plots using point count method. Each plot was surveyed once during the study period (1997–2001), with all surveys carried out by the same observer (JC) during breeding period, between 20th of April and 10th of June. At each plot, a single 20 min point count was conducted from sunrise to 3 h afterwards, during which every bird seen or heard within a 100 m radius plot was recorded (Tellería 1986; Bibby et al. 2000). The restricted 100 m distance enabled us to associate bird abundance with the contiguous area of homogeneous habitat. Given the large sample size (207 plots), we assumed that a single long duration point count (20 min) per plot during the breeding season would be sufficient to detect the majority of territorial species present at each site (Ralph et al. 1995; Sorace et al. 2000; Camprodon et al. 2007). To minimise potential temporal biases among plots with different management strategies or stages, bird surveys followed a stratified sampling design in which plots from each management stage were systematically distributed across sampling years (Camprodon and Brotons 2006). Moreover, a

complementary protocol was applied to detect the presence of woodpeckers, as their contacts are usually scarce when using the standard point count method (Camprodon et al. 2008). In each plot, after completing the 20 min point count, we conducted a complementary 10 min survey that consisted of playing a recording of woodpecker calls for 5 min, followed by a 5 min silent listening period to record species response. During the 5 min of playback, if the response of a woodpecker was heard, the audio was stopped so that it could be correctly identified. Playback included calls of the black woodpecker (*Dryocopus martius*), great spotted woodpecker (*Dendrocopos major*), and Iberian green woodpecker (*Picus sharpei*). We did not include the lesser spotted woodpecker (*Dryobates minor*) nor middle spotted woodpecker (*Dendrocoptes medius*) as Scots pine forests and our study area are out of their distribution range (Camprodon et al. 2007). Detections of the specified woodpecker species were added to the total bird counts. We avoided sampling in windy and rainy days to reduce detectability biases (Tellería 1986). Raptors, exclusive migrant species, and individuals only overflying the plots were excluded from our analyses as point count method is not appropriate to detect them, and their detection may not be associated with forest structure or management type.

According to habitat preferences, we grouped species as either forest specialists or generalists based on the classification of (Díaz et al. 1998) and adapted to other classifications of the Pyrenean bird communities (Gil-Tena et al. 2007; Ameztegui et al. 2018). Forest specialists live exclusively or mainly in forests and forest generalists are those birds that use forested habitats combined with open areas such as shrublands and grasslands. Moreover, with the aim to evaluate changes in the bird community from a more ecological perspective, we divided birds according to their nesting and foraging requirements (Verner 1984). The resulting guilds were canopy, cavity, understory and ground nesters, and trunk, canopy, understory, and ground foragers (Table A.1). Bird community data was treated at two levels: species richness of generalist and specialist forest bird species, and abundance of generalists, specialists, and each guild. Abundance was calculated as the number of territorial specimens detected for each species per plot.

Forest structure data

To characterize the forest structure of all studied plots and management types, we conducted forest inventories at each bird point-count location. Inventories were carried out by the same observer (JC) in the same year as the corresponding bird surveys, but on different days within the same vegetation period (June–July). We conducted three forest inventory plots of 10 m radius, one of them coinciding with

the centre of bird point count and the other two placed 50 m apart in easterly and westerly directions. In all plots, we measured the diameter at breast height (DBH) and the height of all individuals of tree species with DBH > 7.5 cm. Also, understory and canopy cover were visually estimated. Using the mean across the three subplots, we selected a diversity of forest metrics susceptible to vary between UEA and EA management strategies and its corresponding management stages: tree diameter class distribution, GINI index, mean diameter (Dm), dominant height (Ho), tree density (N), basal area, deadwood, and canopy and understory covers (see Table 1 and Fig. A.2). Dominant height was calculated as the average height of the two largest-diameter trees of each plot and basal area was determined using 5 cm diameter classes (Ameztegui et al. 2018). GINI index was used as a measure of heterogeneity based on diameter classes distribution. It is a continuous variable directly related to tree size hierarchy, with values ranging from 0 (perfect equality) to 1 (maximum theoretical inequality), allowing for straightforward interpretation (Lexerød and Eid 2006; Valbuena et al. 2012). Moreover, we quantified lying deadwood volume and snag density with a transect of 400 m length and 2 m width at each bird point count plot (Ståhl and Lämås 1998). To do so, the diameter of fallen logs was measured at their basis and the length up to 7.5 cm, and then a standard form factor was applied.

Data analysis

We used Wilcoxon tests to descriptively compare structural variables (as stand descriptors) between UEA and EA strategies and their management stages, ensuring that their differentiation according to the management approach was statistically supported (see Fig. A.3 and Fig. A.4). To evaluate the differences in bird community between management strategies, we fitted Generalized Linear Mixed Models (GLMM) for each response variable (species richness and abundance of forest generalist and forest specialist birds and abundance of each guild) with management strategy and bioclimatic region as predictor variables. We included bioclimatic region as a covariate to account for potential variability in bird community composition across the distribution and altitude range of the plots. Moreover, as plots were grouped within stands, we incorporated “stand” as a random factor to reduce spatial autocorrelation. Year of monitoring was also included as a random factor to control the interannual variability in bird abundances and detectability. The same GLMM structure as described above was used to analyse generalist and specialist bird richness and abundances and each guild abundance among management stages (six levels: E_You, E_Pre, E_Sed, E_Fin, U_Dec, and U_Cap). Pairwise post-hoc comparisons were

performed using Tukey’s Tests (Tukey 1949). E_You was excluded from the trunk foragers model as they were nearly absent, and the model did not converge.

To explicitly evaluate whether bird communities were better explained by management-based categories or by structural variables (direct descriptors of forest conditions), we fitted a parallel set of models based on forest structural variables. For the structural variables models, we first checked collinearity among a set of forest structural variables that can influence bird community. We discarded correlated variables with a Spearman’s rank correlation coefficient $\rho > 0.7$ (e.g. basal area), resulting in a final set of six representative structural variables: GINI index, mean diameter, dominant height, tree density, canopy cover, and understory cover (Fig. A.5). Deadwood was excluded from the final models, as preliminary analyses indicated a low explanatory power for this variable (see Fig. A.6). We then built a full GLMM for each response variable (generalist and specialist bird richness and abundance and each guild abundance), including the set of six scaled structural variables and “stand” and “year” as random factors. Using the *dredge* function from R-package MuMIn (Barton 2023), we generated all possible combinations of these structural variables and selected the most parsimonious models according to Akaike information criterion corrected for small sample size scores ($\Delta \text{AICc} < 2$, (Burnham and Anderson 2002). We then built the best model for the selected structural variables and included bioclimatic region as a covariable.

In exploratory analyses, we also evaluated models combining management categories (management strategy or management stage) with continuous structural variables. Because management categories represent practical proxies of forest structure and developmental conditions, their simultaneous inclusion with a set of structural variables resulted in convergence issues and reduced interpretability. We therefore treated management-based and structure-based approaches as alternative, mutually exclusive representations of forest conditions and compared their explanatory power using separate models. Finally, we compared the differences in the AICc scores ($\Delta \text{AICc} < 2$) between the management strategy, management stage, and structural variables models and the null model containing only the intercept. To process the GLMMs, we used the *glmmTMB* function from R package glmmTMB (Brooks et al. 2017). Since bird data were counts, we used a Poisson error distribution, or a Conway-Maxwell Poisson distribution when data had over- or under dispersion (Shmueli et al. 2005; Sellers 2023).

Moreover, to account for the dependence of species richness on the sampling effort in each management strategy and stages (different number of plots), we checked species richness at equivalent levels of sampling coverage using

DataInfo and *estimateD* functions from iNEXT package (Chao et al. 2014; Hsieh et al. 2016). Coverage-based rarefaction was performed at a standardized sample completeness level (0.95) corresponding to the minimum observed sample coverage across assemblages.

All data exploration and analysis were performed at the plot level using *R software 4.3.1* (R Core Team 2023) and considering significant relationships at p -values < 0.05 . Outliers and homogeneity of variance were checked in data exploration following (Zuur et al. 2010).

Results

A total of 34 bird species were recorded in the study plots, among which 20 species were considered as forest specialists (Table A.1). Total average bird richness per plot was 8.75 (minimum of 1 and maximum of 17), with an average bird abundance of 11.07 (3–21) individuals. Forest specialist richness was on average 5.31 (0–11) and abundance was 6.52 (0–16).

The most abundant nesting guild was understory nesters followed by cavity nesters and overstory nesters (mean = 4.44, 3.28 and 2.42 respectively), whereas ground nesters were comparatively scarce (mean = 0.66). Among the foraging guilds, overstory and understory foragers were the most abundant (mean = 5.82 and 3.30 respectively). Ground foragers and trunk foragers showed lower abundances (mean = 1.03 and 0.64 respectively).

Comparing bird community between UEA and EA

Forest specialist bird richness and abundance was significantly higher in UEA than EA plots. Species richness of forest specialist was also higher in the Oreoborealoide bioclimatic region. Forest generalist species showed the same

patterns, with higher richness and abundance in UEA than EA and bioclimatic region being significant at abundance level (Table 2) with higher values in the Oreoborealoide region. Standardized richness estimates at equal sample coverage revealed no differences between management strategies (Table A.2).

Bird guilds showed different responses. Cavity nesters, overstory foragers, and understory nesters and foragers showed differences between management strategies, being significantly more abundant in UEA compared to EA plots. The remaining bird guilds did not show significant responses between management strategies. However, we found an effect of bioclimatic region on cavity nesters, overstory nesters, ground nesters, and trunk and understory foragers, all with higher values in Oreoborealoide region except for ground nesters.

Differences across management stages

Forest specialist species richness was minimum in E_You (mean richness of 3.08), whereas in U_Cap (8.48) and E_Pre (6.60) we found the maximum values. U_Dec, E_Sed, and E_Fin showed similar levels. In terms of forest specialists abundance, the results had the same patterns as for forest specialists richness. Regarding generalist species, we did not find differences among management stages except for E_You (2.08), where we found significant less species. E_Pre had the highest abundance of generalist birds (5.37) compared to the other EA stages, but without significant differences with UEA stages (Fig. 2 and Tables from A.3 to A.6). On the other hand, E_You (2.69) had the lowest abundance compared to E_Pre and UEA management stages (U_Dec and U_Cap). Sample coverage values were consistently high across groups (Table A.7), supporting the adequacy of sampling effort and indicating that observed

Table 2 For each response variable, mean values comparison between EA and UEA strategies and estimate, standard error (SE)

Bird group		Mean EA vs. UEA	Estimate	SE	<i>P</i> -value	Bioclimatic region
Forest specialist	Ric.	4.57–6.73	0.532	0.098	<0.001 ***	Ore **
	Abu.	5.62–8.25	0.496	0.100	<0.001 ***	Ns
Forest generalist	Ric.	2.90–3.37	0.196	0.069	<0.010 **	Ns
	Abu.	3.91–4.52	0.248	0.084	<0.010 **	Ore **
Cavity nesters		3.08–3.66	0.495	0.176	<0.010 **	Ore ***
Overstory nesters		2.40–2.60	0.222	0.127	0.084	Ore *
Understory nesters		3.69–5.87	0.576	0.098	<0.001 ***	Ns
Ground nesters		0.63–0.70	-0.464	0.293	0.114	Nem ***
Trunk foragers		0.60–0.73	0.535	0.397	0.177	Ore *
Overstory foragers		5.24–6.93	0.355	0.099	<0.001 ***	Ns
Understory foragers		2.99–3.89	0.410	0.097	<0.001 ***	Ore *
Ground foragers		0.97–1.15	0.152	0.161	0.345	Ns

P-value (significant ones in bold), and significance level of the Bioclimatic region in the GLMMs comparing both strategies. Significance level = *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

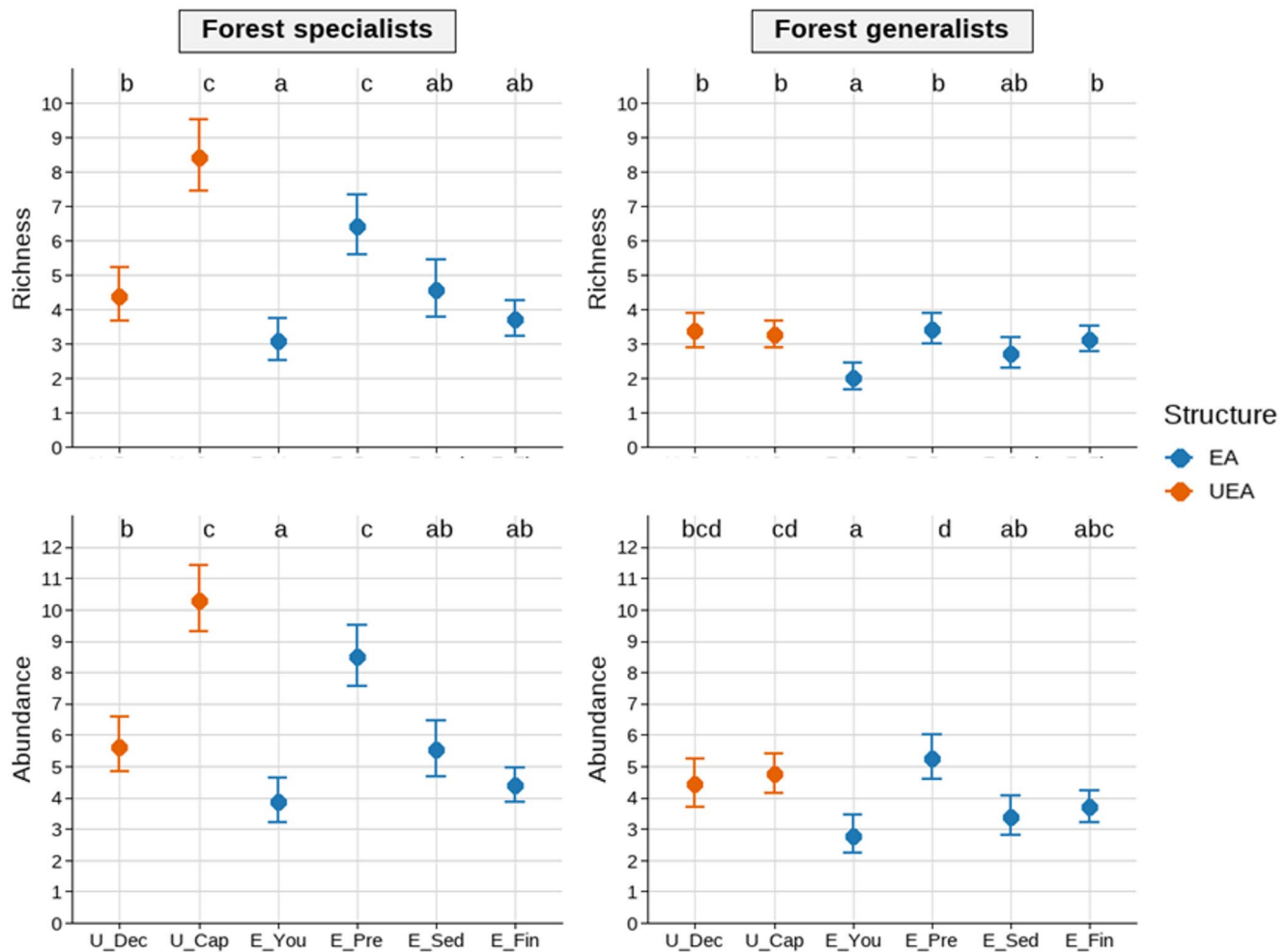


Fig. 2 Differences in observed richness and abundance of forest specialist and generalist bird species across management stages. Differences were based on Tukey's Test where stages with the same letter

indicate non-significant differences. Lower and upper whiskers indicate the 2.5% and 97.5% quartiles, and the blue dot indicates the estimated marginal mean value

differences in richness were not driven by unequal sampling completeness.

E_You also had the lowest abundance of every nesting guild, except for ground nesters, that were significantly higher in E_You and E_Fin, although this guild had considerably low abundances in all management stages (Fig. 3 and Tables from A.8 to A.11). Cavity nesters were more abundant in U_Cap and E_Pre and finding the minimum abundances in E_You and U_Dec. For overstory nesters, the major abundance was found in E_Pre, whereas for understory nesters, both stages (U_Dec and U_Cap) of UEA management strategy had the higher abundances, particularly U_Cap.

Foraging guilds showed varied responses. Trunk foragers were almost absent in U_Dec, E_Sed, and E_Fin, showing significant differences with U_Cap and E_Pre. A similar pattern was found for overstory foragers, but with E_You also being lower than E_Sed, E_Pre, and U_Cap (Fig. 4 and

Tables A.12 to A.15). Understory foragers were higher in U_Cap and E_Pre as well, but they only significantly differed from E_You and E_Fin. E_You also had less understory foragers than U_Dec. Finally, for ground foragers we did not find any differences across management stages.

Bioclimatic region did not influence differences between management types and forest and generalist birds. Among bird guilds, bioclimatic region only had significant influence on overstory nesters and ground nesters, which were more abundant in Oreoborealoide and Nemoral regions respectively.

Bird community response to structural variables

Among the 6 structural variables considered, canopy cover was the most selected (8 times) for the models of each response variable, followed by mean diameter (Dm, 7 times) and dominant height (Ho, 6 times). On the other hand, tree

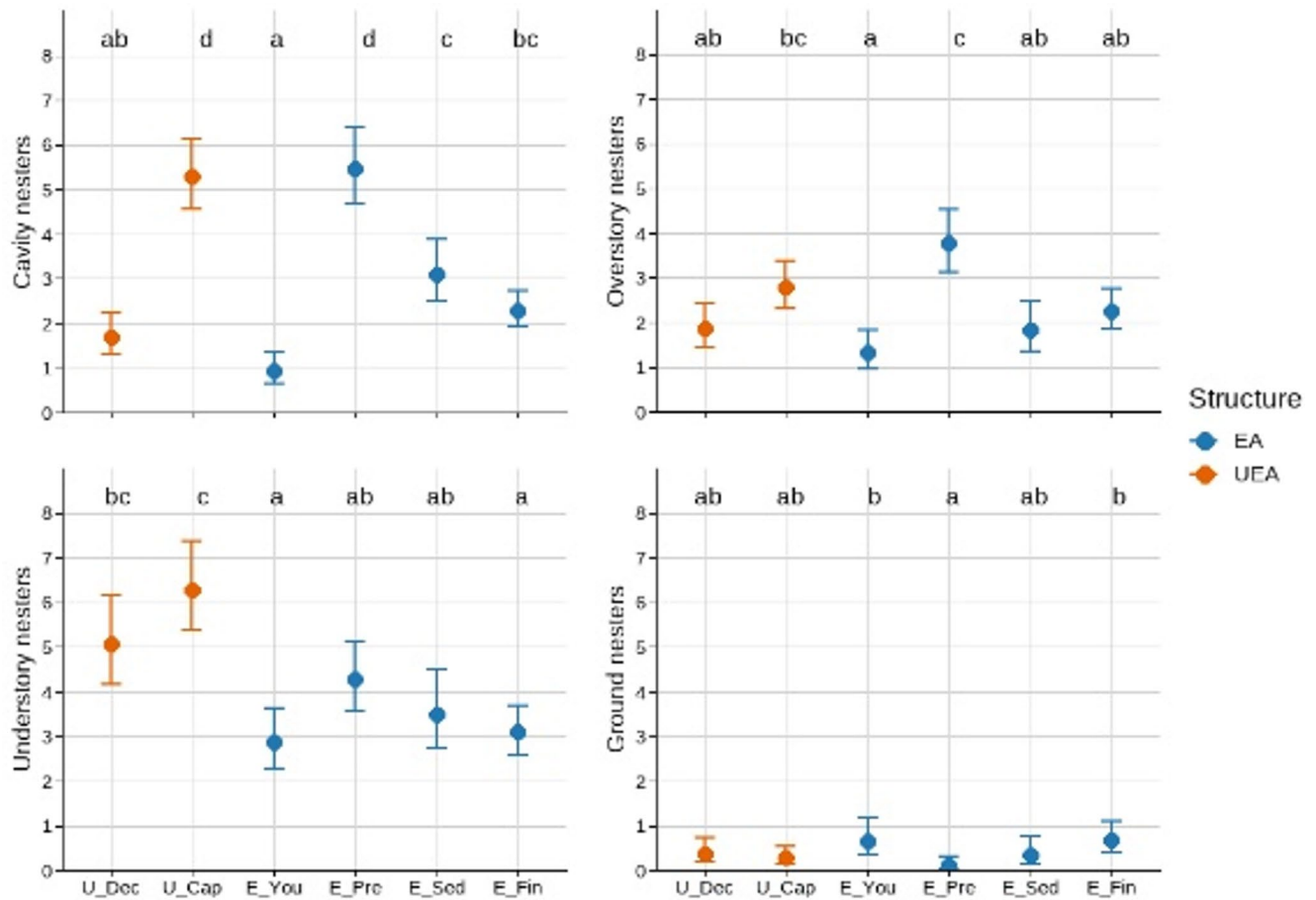


Fig. 3 Differences in observed abundances of nesting guilds across management stages. Differences were based on Tukey's Test where stages with the same letter indicate non-significant differences. Lower

and upper whiskers indicate the 2.5% and 97.5%, and the blue dot indicates the estimated marginal mean value

density (N, 2 times) was the less influential variable for bird community (Table 3 and Table A.16). However, when selected, GINI index has the stronger effects in the models.

Forest specialists differed from forest generalists, selecting canopy cover and dominant height, whereas generalists selected understory cover, density, and GINI index at both richness and abundance levels. Bird guilds showed varied responses, highlighting that all foraging guilds selected canopy cover.

Model selection comparing management strategy, management stages and forest structural variables

Comparing the fitted models of management strategy, management stage, and best structural variables by AICc, we found that management stage was the best predictor for bird community in Mediterranean Scots pine forests for most of the response variables. In this sense, management stage was the most predictive factor for all forest specialist richness and abundance and forest generalist abundance as well as

most bird guilds. Only in the case of forest generalist richness, understory foragers, and ground foragers the best model was the structural variables model (Table 4).

Discussion

Bird community response to management strategy and management stage in scots pine forests

The aim of this study was to compare the effect of even-aged (EA) and uneven-aged (UEA) forest management strategies on bird communities in Scots pine forests to assess the relative influence of management strategy, management stages, and forest structural attributes. Our results show that UEA forest strategy harbours higher species richness and abundance of both forest specialist and forest generalist bird species compared to EA forests, consistent with observations in European beech forests by (Schall et al. 2018). Even though, bioclimatic region also had a significant effect on

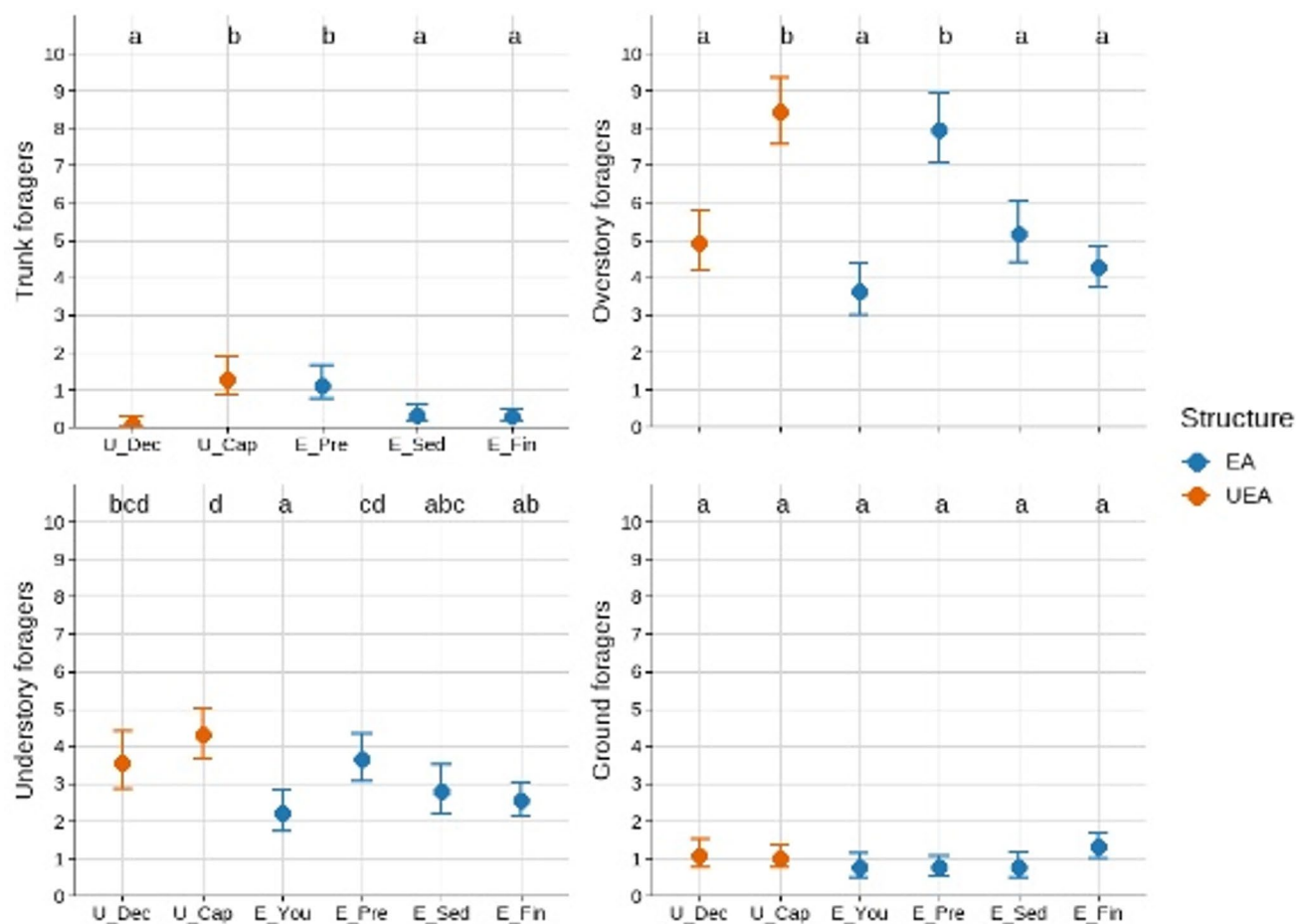


Fig. 4 Differences in observed abundances of foraging guilds across management stages. Differences were based on Tukey's Test where stages with the same letter indicate non-significant differences. Lower

and upper whiskers indicate the 2.5% and 97.5%, and the blue dot indicates the estimated marginal mean value

Table 3 Estimates of the explanatory variables included in the selected GLMMs for each response variable and structural variables

Bird group		GINI	Dm	Ho	N	Can. cv.	Und. cv.	R ² con.	R ² mar.	NP
Forest specialist	Ric.	1.50	0.02	0.03		0.01		0.25	0.17	7
	Abu.		0.01	0.04		0.01		0.20	0.12	6
Forest Generalist	Ric.	1.24	0.01		0.01		0.01	0.07	0.06	7
	Abu.	1.51	0.02		0.01		0.01	0.09	0.06	7
Cavity nesters		1.93	0.04	0.05		0.01		0.42	0.34	7
Overstory nesters			0.02	0.02				0.20	0.07	5
Understory nesters						0.01	0.01	0.21	0.08	5
Ground nesters				-0.07				0.68	0.35	4
Trunk foragers		2.75	0.07			0.02		0.80	0.25	6
Overstory foragers				0.05		0.01		0.17	0.10	5
Understory foragers						0.01	0.01	0.19	0.10	5
Ground foragers						-0.01	0.01	0.19	0.08	5

R² conditional, R² marginal, and number of parameters (NP) of the model are shown

bird community patterns indicating that management strategy can have a contextualized effect on birds. Richness and abundance of forest specialists and generalists were greater in the Oreoboraloide region than in the Nemoral region.

However, since UEA forests were mostly located in the Nemoral region and EA forests were more evenly distributed across regions, the observed differences between management strategies are not attributable to geographic patterns

Table 4 comparison of the fitted models for each response variable

		NULL	Management strategy	Management stage	Structural variables
Forest specialist	Ric.	916.8	863.3	810.2	828.4
	Abu.	988.4	956.6	889.1	922.6
Forest generalist	Ric.	712.7	653.7	642.1	638.4
	Abu.	838.4	817.8	800.1	804.6
Cavity nesters		825.6	797.8	715.3	733.9
Overstory nesters		741.2	733.2	716.2	725.3
Understory nesters		879.2	832.0	829.2	829.6
Ground nesters		415.4	402.1	394.0	395.2
Trunk foragers		341.4	339.5	287.6	322.4
Overstory foragers		939.2	931.0	874.7	899.2
Understory foragers		756.1	742.8	736.0	721.4
Ground foragers		522.7	524.4	522.8	518.5

AIC of the null model and AICc for the independent models of management strategy, management stage, and the set of selected structural variables are shown. Selected best models are highlighted in bold

contained in the Bioclimatic variable alone. Moreover, While GLMM results indicated higher local species richness in UEA forests, coverage-based rarefaction revealed no differences in standardized richness between management strategies. This suggests that both strategies host a similar regional species pool, and that observed differences arise from local management related processes rather than from differences in species availability.

UEA and EA management strategies encompass different management stages among which the Young even-aged stands (E_You) were the poorer in terms of forest specialists and generalists at both richness and abundances levels. This aligns with findings of Savilaakso et al. (2021), who reported reduced bird richness in young EA forests than in older EA or UEA. They also found that young EA forests can provide habitat for opportunistic and open habitat species, whereas it is less suitable for forest dependent species. Even though, our results suggest that even generalists are less abundant in E_You, likely due to the heavy structural simplification of these stands: dense, homogeneous with small trees (DBH < 25 cm), low canopy stratification, and poor understory development.

The highest richness and abundances of forest specialists were observed in U_Cap and E_Pre stages. U_Cap represents the least intensive managed stage among the studied ones, with management treatments that allow retaining some medium to large diameter trees, while maintaining a more heterogeneous forest structure (Kuuluvainen et al. 2012 b) (see Fig. A.1). Similarly, E_Pre, despite having a similar average tree diameter than other management stages, they have a high proportion of medium-sized trees as they have not yet undergone intensive harvesting. These stands

maintain a high density that promotes competition and decay of less vital trees while maintaining a higher canopy cover than other EA management stages (Ibarra et al. 2020). Thus, this management stage seems to be as suitable as U_Cap stands for forest birds (Ameztegui et al. 2018; Versluijs et al. 2020). In contrast, U_Dec, which are more intensively harvested, showed lower richness and abundance of forest specialist birds compared to U_Cap, supporting the hypothesis that management intensity affects forest specialists more than generalists (Paillet et al. 2010). In line with this, we found that generalist bird richness did not differ among management stages, regardless of the management strategy. Forest specialists would benefit from management practices that result in balanced and well-developed tree canopies. This may be linked to reduced foraging effort in species such as *Regulus sp.*, compared to other generalist species that may be more adaptable to management stages with more widely spaced trees and more compressed or depressed canopies resembling edge conditions (Kotsonas and Bakaloudis 2025). For E_Fin, our results are consistent with (Ameztegui et al. 2018), highlighting that this management stage is not suitable for forest specialist species. Hence, due to its open structure characterized by a herbaceous-dominated ground layer interspersed with shrub patches, this management stage could favour open habitat species rather than forest specialists (Kellner et al. 2016).

Different responses of bird guilds to management strategy and management stage

As expected, the response of bird guilds varied across management strategy and stages, reflecting their specific ecological requirements (Balestrieri et al. 2015; Perry 2017; Ameztegui et al. 2018; Basile et al. 2019). UEA systems promote structurally heterogeneous stands usually maintaining late-successional features as large diameter trees, that provide habitat sources for cavity nesting birds (Kuuluvainen et al. 2012; Balestrieri et al. 2015). Moreover, UEA strategy maintains canopy cover in the long term and enhances vertical stratification and diversity in tree height which supports both canopy and understory dependent species (Szmyt 2025). These features may explain the higher abundance of cavity nesters, overstory nesters, and understory nesters and foragers in UEA managed forests.

Among the guilds, cavity nesters showed the strongest response to management stage as we hypothesized (Ameztegui et al. 2018; Pakkala et al. 2024). Early EA stages (E_You) resulted unsuitable for cavity nesters due to their young, homogeneous structure, and scarcity of trees suitable for cavity excavation or decay-formed cavities (Robles et al. 2011). Likewise, U_Dec also had low abundance of cavity nesters. Despite the fact they are UEA, these stands

have historically experienced intensive harvesting removing the largest trees and thereby limited cavity availability, which strongly depends on the presence of large trees, stand age and varies among forest types (Löhmus et al. 2005; Paillet et al. 2017). Conifer species are less prone to cavity formation due to decay processes compared to deciduous species, and therefore cavity availability in Scots pine forests depends more on primary cavity excavators (Remm and Löhmus 2011). E_Pre and U_Cap are the management stages hosting more cavity nesters, as well as trunk foragers and overstory nesters and foragers. Trunk foragers, which included only woodpeckers, depend on tree trunks both for foraging and for excavating nesting cavities. They are widely described as late-successional forest indicators and being negatively influenced by forest management (Walankiewicz et al. 2011; Balestrieri et al. 2015; Ameztegui et al. 2018; Basile et al. 2021b). In our study, these species were detected exclusively, although in low abundances, in U_Cap and E_Pre. This pattern suggests that, within the studied managed Scots pine forests, these stages represent the closest to mature conditions, including greater availability of large trees and denser canopy cover, which may also benefit overstory nesters and foragers, even though they do not fully correspond to true old-growth conditions. (Gutzat and Dormann 2018). Nonetheless, we would have expected to find also high abundances of overstory nesters in E_Sed, as (Ameztegui et al. 2018) found. This might be explained by the lower canopy cover and tree density in our E_Sed stands, which could increase predation risk and reduce nesting site availability for canopy-dwelling birds (Pettersson et al. 1995; Balestrieri et al. 2015).

Management stage better predicts bird community in Scots pine forests

We hypothesized that the abundance of certain guilds such as those *a priori* associated with specific vertical strata (overstory or understory), would be better explained by structural attributes rather than by management stage or strategy categorical variables *per se* (Canterbury et al. 2000). This hypothesis was partially supported. In the case of understory foragers, the model including canopy and understory covers performed best, indicating that these structural attributes are stronger predictors of their abundance than the management framework. In contrast, overstory guilds were more strongly influenced by management stage. While canopy cover explained variation in overstory foragers, overstory nesters were better predicted by mean diameter and dominant height (see Table 3). These differences likely reflect guild composition: overstory foragers included several secondary cavity nesters (e.g., tits, treecreepers, Eurasian nuthatch) for which large trees are also key factors

(Balestrieri et al. 2015). Notably, similar abundances of overstory species were found in E_Sed, E_Fin, and U_Dec despite marked differences in canopy cover, suggesting that other management stage related factors may influence these guilds (Table 1 and Fig. A.2). For ground foragers, canopy cover and understory cover were selected in the structural variables model. Canopy cover was negatively related with this guild, consistent with the ecology of the four forest generalist species that compose this guild, that often feed in open areas with some bush coverage (see Table A.1) (Lešo et al. 2019). Unlike other guilds, ground foragers showed no significant differences across management stages or strategies, making structural variables the strongest predictors (Versluijs et al. 2020). Nevertheless, the low number of detections for this guild may have limited our ability to detect management effects.

Mean diameter, GINI index, canopy cover, and dominant height were positively associated with cavity nesters and trunk foragers. However, despite their known dependence on specific structural elements (Camprodon et al. 2008; Paillet et al. 2018), management stage still outperformed the structural variables model. This suggests that the categorized management stage may integrate not only measurable structural variables but also factors such as the presence of senescent trees or food availability, which are harder to quantify but ecologically relevant (Robles et al. 2011; Cockle et al. 2011). For instance, although U_Cap forests had only moderate mean diameters, they included trees larger than the site average, a condition favourable for primary cavity excavators such as woodpeckers (Basile et al. 2020), which in turn facilitate habitat for secondary cavity users (Gutzat and Dormann 2018).

Overall, UEA tended to support both forest specialists and generalists better than EA. Yet, in Scots pine forests, management stage was the primary driver of bird community composition, aligning with our finding that the two most favourable stages for birds (U_Cap and E_Pre) belong to different management strategies. This may explain why studies like (Versluijs et al. 2020) in boreal forests, which compared EA and UEA at only a single stage, reported no significant differences between strategies. Additionally, differences in rotation periods and time since treatment between strategies may also contribute to these patterns (Savilaakso et al. 2021).

Management implications and applied conclusions

This study highlights that, overall, UEA management strategy provides more suitable conditions for the bird community inhabiting Scots pine forests than the even-aged (EA) approach. These differences between management strategies were mostly in line with guild responses, with most groups

being more abundant in UEA. However, our results also demonstrate that no single management strategy is universally optimal, and that management stage displays a crucial role in shaping bird assemblages (Ameztegui et al. 2018; Nolet et al. 2018). From an applied forest management perspective, we highlight that bird conservation outcomes are more effectively improved by focusing on the timing and characteristics of specific management stages than by prioritizing broad management strategies or relying solely on forest structural variables as direct descriptors.

Despite UEA forest management maintains canopy cover and a heterogeneous age-class structure over time, our findings indicate that its application does not guarantee high habitat quality (Doyon et al. 2005), as exemplified by U_Dec stands. On the other hand, in EA systems, certain stages such as E_You clearly constrain bird assemblages. Nevertheless, targeted thinning in these young stands can accelerate structural development and enhance future biodiversity potential (Dodson et al. 2012). In more advanced EA stages (E_Sed and E_Fin), low tree density, reduced canopy cover, and scarcity of large trees appear to limit habitat suitability for most forest guilds, although these conditions may favour migratory or open-habitat species (Perry and Thill 2013; Kellner et al. 2016; Ameztegui et al. 2018). Yet, this structural configuration is ephemeral, so the stands will lose their attractiveness for open-habitat birds once regeneration grows or if too many trees are left and there is no bare ground (George et al. 2019; Bakx et al. 2020; Graser et al. 2025). Therefore, when the primary goal is the conservation of forest biodiversity, uneven-aged management appears to be more favourable, since it provides forest maturity attributes and maintains structural heterogeneity.

Given the heterogeneity of responses observed across guilds and management contexts, several authors have suggested combining EA and UEA systems to promote spatial heterogeneity and biodiversity at the landscape scale (Doyon et al. 2005; Schall et al. 2018, 2020; Savilaakso et al. 2021). Our results partially support this view, as neither strategy proves universally optimal. The effectiveness of any forest management approach depends largely on forest type and socio-economic context (Chaudhary et al. 2016).

As all studied forests are managed and remain far from reference or mature conditions, adopting a landscape perspective that integrates both strategies while prioritizing biodiversity-rich management stages (e.g., U_Cap and E_Pre) could help mitigate these limitations in multifunctional forests (Schall et al. 2020). At the same time, less favourable stages should be spatially limited and embedded within a matrix of higher-quality stands following the Triad approach (Duflo et al. 2025), although implementing such planning remains challenging in the Pyrenean context due

to highly fragmented and predominantly private forest ownership (Vaccaro 2005).

To this end, naturalistic silviculture, applied at the stand level and emphasizing the retention of high-quality future trees and individuals with biodiversity potential, enhances stand heterogeneity while aligning with conservation objectives within a multifunctional forest management framework (Beltrán et al. 2020). Such an approach should be guided by the principles of Closer-to-Nature Forest Management and align with the objectives of the EU forest and biodiversity strategies for 2030 (European Commission 2021a, b; Larsen et al. 2022), incorporating best-practice guidelines, that include extending rotation periods, maintaining continuous forest cover, promoting species diversity, retaining key structural elements (e.g., large trees, deadwood, and micro-habitat trees), and ensuring the presence of mature forest stands with natural dynamics that act as forest biodiversity reservoirs (Vandekerckhove et al. 2011, 2013; Motta et al. 2014; Basile et al. 2021b).

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Declarations

Competing interests The authors declare no competing interests.

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