

Bird community response in mountain pine forests of the Pyrenees managed under a shelterwood system



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ABSTRACT

Understanding the effects of forest management on biodiversity is a vital challenge given the current regime of large-scale socio-ecological drivers affecting forest ecosystems and their multifunctionality. Here we assessed how forest management affects abundances of common breeding birds in mountain pine (*Pinus uncinata* Ram. ex DC) stands in the Pyrenees. We assessed, at guild level, avian response to changes in stand structure across different management stages in forests managed under a shelterwood system, as well as in unmanaged forests. Bird guilds were based on habitat breadth, nesting habitat, and foraging habitat. Bird abundance was modelled separately for each guild as a function of stand variables known to be good surrogates of stand density (stand density, quadratic mean diameter, shrub cover) and maturity (dominant height, cavities). For this purpose, we used likelihood methods, which provided flexibility in the shape of the expected responses. For most bird guilds, unmanaged forests showed similar bird abundance to managed forests. Total bird abundance was maximum after regeneration cuts, due to the positive response of canopy nesters and canopy foragers. The typical open stand structure after removal cuts negatively impacted forest specialists, cavity nesters and trunk foragers, but the impact was offset by the higher number of generalists, ubiquitous, ground nesters and ground foragers. General stand descriptors such as stand density, quadratic mean diameter and dominant height were the most influential variables, whereas the association of bird abundance with shrub cover and cavities was less influential and guild-specific. We show that a shelterwood system can be a suitable management tool to promote the abundance of most common bird guilds in dense, homogeneous stands, given that some key structural legacies are retained throughout the rotation and stand structure heterogeneity is promoted. By obtaining quantitative relationships between the main structural features affected by harvests and the abundance of birds, we formulate management recommendations that are valid for forests managed not only under shelterwood systems but also under other silvicultural methods.

1. Introduction

The forests of the Pyrenees, like those of most mountains in the Mediterranean basin and Western Europe, have a long history of overexploitation dating back millennia. This trend has drastically reversed since the second half of the 20th century, as depopulation and other socio-economic changes have brought abandonment of farmland, decline in livestock, and widespread desertion of logging and forest

management (García-Ruiz et al., 1996; Cervera et al., 2015), all leading to forest expansion (Roura-Pascual et al., 2005; Ameztegui et al., 2010).

Despite a lack of management for decades, most forests in the region are relatively young and still more conditioned by land-use legacies than by natural disturbance dynamics (Ameztegui et al., 2016). Therefore, they do not present the complex structural features that can be found in natural or old-growth forests in other parts of the world (Wirth et al., 2009; Barbati et al., 2012; Mansourian et al., 2013).

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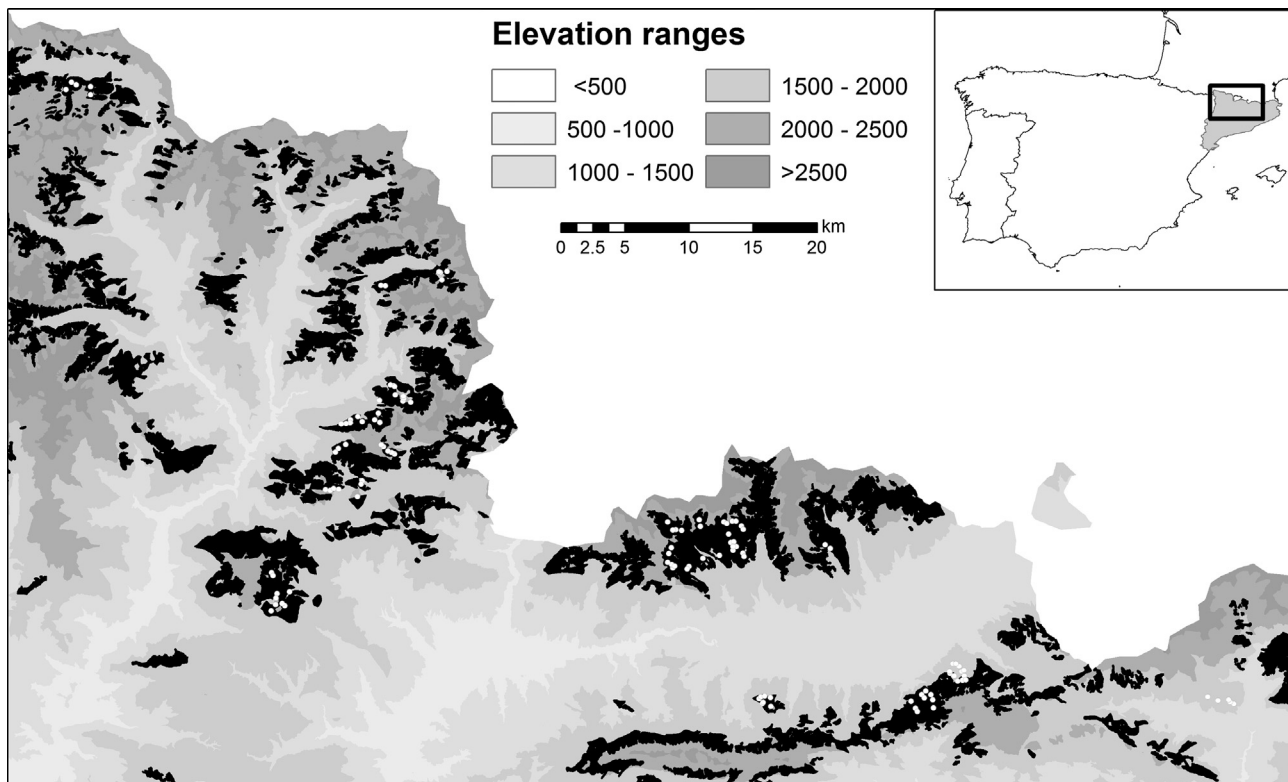


Fig. 1. Study area (upper right) and plot location (white dots) within the mountain pine distribution (in black).

Consequently, current landscape is characterized by large areas of continuous, even-aged forest cover, often with high stem densities (Coll et al., 2012). These homogeneous landscapes are highly vulnerable to natural disturbances (Martín-Alcón et al., 2010) and can compromise the provision of goods and services supplied by forests, including their ability to host biodiversity (Gil-Tena et al., 2007; Moreira and Russo, 2007). For instance, several bird species require heterogeneous stand structures—with vertical stratification—to meet their requirements for foraging and nesting substrates (Bergner et al., 2015; Mag and Ódor, 2015), whereas several other bird species need a mosaic of open areas and forests to thrive, and are currently endangered due to forest expansion (Vallecillo et al., 2008).

In this context, forest management can help break the landscape homogenization process by modifying forest structure and diversifying habitats (Perry and Thill, 2013; Duguid et al., 2016). Of the many silvicultural systems available, most managers of pine forests in the Pyrenees use a shelterwood system. The shelterwood system is applied through a series of partial cuts that progressively remove the entire stand over a fraction of the rotation, usually 20–40 years (Smith et al., 1997), promoting the establishment of a new generation of seedlings before the mature trees are fully removed. Cuts are usually applied on relatively small surfaces (a few hectares), and the method also avoids the period completely devoid of trees that characterizes other silvicultural systems. For all this, the shelterwood system is suggested to favour avian diversity (Goodale et al., 2009; King and DeGraaf, 2000), particularly when applied on small groups (Balestrieri et al., 2015) and if the rotation period and/or proportion of shelter trees are increased (Mag and Ódor, 2015).

Some of the key structural features of forests—such as tree density, basal area, dominant height or understory development—vary significantly throughout the rotation of a forest managed under shelterwood systems. Birds are a taxon particularly responsive to changes in forest structure (Camprodon and Brotons, 2006; Gil-Tena et al., 2007; Nikolov, 2009), but the structure resulting from each management stage affects avian diversity in a guild-specific way depending on the

functional requirements of its organisms (e.g. Balestrieri et al., 2015; Mag and Ódor, 2015). However, the direct relationship between the main forest structural features and avian diversity over time is not yet well known.

Here we analyzed bird communities across a geographical gradient of mountain pine (*Pinus uncinata* Ram. ex DC) forests in the Pyrenees. We sampled bird abundance at three different stages in the rotation of forests managed as a shelterwood system, as well as in unmanaged stands. This approach captured the full range of forest structural variability throughout rotation. Our aim was (i) to assess abundance variability in several bird guilds—based on habitat specialization and nesting and foraging substrates—across successive management stages, and (ii) to quantify and model the relationship between the main structural features that are modified by management and the abundance of different bird guilds. Given that shelterwood cuts gradually modify several key features of forest structure at relatively small spatial scales and relatively long timespans of decades, our hypothesis is that the progressive reduction in stand density will not substantially affect bird abundance provided that key nesting and foraging resources are maintained. However, the drastic changes in forest structure after the removal cuts are likely to induce sharp changes in the avian community.

2. Materials and methods

2.1. Study area and surveyed stands

Our study area was the subalpine mountain pine forests of the Catalan Pyrenees. Mountain pine (*Pinus uncinata* Ram. ex DC) is a shade-intolerant, soil-indifferent conifer dominating the subalpine belt of the southern Pyrenees between 1700 and 2400 m a.s.l., where it covers over 60,000 ha (Coll et al., 2012). Mountain pine forests constitute favourable habitats for a large community of plant and animal species, and have been classified as Habitat of Community Interest (92/43/EEC) when distributed on siliceous substrates (habitat code 9430)

and as a Priority Habitat when they thrive over gypsum or limestone (habitat code 9430^{*}).

A total of 120 stands were surveyed across the range of mountain pine forests over siliceous substrate in the Catalan Pyrenees (Fig. 1). Stand size ranged between 5 and 15 ha. All stands surveyed were public-owned and ca. 120 years old, with some trees reaching 150–180 years. Of the 120 stands surveyed, 30 were established in forests that had not been managed for at least five decades, whereas 90 were managed according to a shelterwood system. The shelterwood system implies a series of progressive cuts that lead to the establishment of a new generation of seedlings before the mature trees are fully removed. Once the regeneration is established, subsequent cuts give the new seedlings more light and growing space. Shelterwood systems usually include three types of cuts: (i) preparatory cuts, that aim to promote crown development by reducing tree density; (ii) establishment or regeneration cuts, that aim to promote establishment of a new generation of seedlings; (iii) one or more removal cuts, when the remaining mature trees are removed to give more light and growing space to the new generation of seedlings. In the case of *Pinus uncinata* in the region, rotation is around 150 years, and the shelterwood systems usually include one preparatory cut, one regeneration cut, and one or two removal cuts, depending on site quality (Beltrán et al., 2014). As cuts are applied over a period of 30–40 years, the 90 managed stands were sampled at different stages of this period to ensure a broad range of forest structures to test their effect on bird abundance: 30 stands were sampled after preparatory cuts, 30 were surveyed after regeneration cuts, and 30 were surveyed after the last removal cut, when few mature trees were left and successful regeneration had been observed.

2.2. Bird surveys and guild categories

Bird surveys were carried out once in each of the 120 stands from May to June in 2005 and 2006. We applied the point-count method with limited distance (Tellería, 1986; Bibby et al., 1992) as it usefully relates bird abundance to vegetation structure and is adaptable to relatively small areas of homogeneous habitat. Habitat structures with diverging forest stand density may introduce bias in the study due to the different visibility in each habitat type (Bibby and Buckland, 1987). Nevertheless, most of the records were aural detections, and previous analyses showed that the abundance of the birds that were more difficult to detect was similar using a 25 m radius or a 100 m radius. Therefore, we decided to use the data of the 100 m radius, since it allowed better estimates of the abundance of birds with larger territories, underestimated if we used a smaller radius (Camprodon and Brotons, 2006; Camprodon et al., 2008). Surveys were carried out by the same observer (JF) early in the morning, from sunrise to three hours afterwards, and in the absence of rain and strong wind. The 100-m-radius point-count was surveyed during 20 min in which aural and visual detections were registered (Camprodon and Brotons, 2006; Camprodon et al., 2008). In the case of Black Woodpecker (*Dryocopus martius*), point-counts were complemented with other evidences of presence such as cavity holes or feeding trails due to its large home range. Therefore, wherever the species had not been contacted (i.e. no record during the point-count) but we observed holes or trails we assumed it was present in the plot and we assigned an abundance of one individual. Raptors, common raven (*Corvus corax*), carrion crow (*Corvus corone*) and cuckoo (*Cuculus canorus*) were neither recorded nor considered in the analyses due to the unsuitability of the survey method to properly estimate their abundance.

We assessed total and per-guild bird abundance based on habitat breadth and main nesting and foraging preferences within the stand (Table 1). According to habitat breadth, birds were classified as either specialists, generalists or ubiquitous, adapting previous classifications (Díaz et al., 1998; Gil-Tena et al., 2007; Gil-Tena et al., 2009) to the avian communities in the Catalan Pyrenees (see Table A1 in the

Table 1

Descriptive statistics of bird guild abundance in mountain pine forests according to habitat breadth, nesting habitat and foraging habitat, and the main explanatory variables considered as potential predictors. The selected predictors are shown in bold.

	Variable	Units	Mean	Range (min–max)
BIRD ABUNDANCE	Specialists (Habitat breadth)	#	11.18	1–20
	Generalists (H)	#	8.09	1–19
	Ubiquitous (H)	#	0.41	0–6
	Cavity (Nesting habitat)	#	8.80	0–18
	Canopy (N)	#	7.10	1–18
	Understory (N)	#	2.46	0–9
	Ground (N)	#	1.32	0–9
	Trunk (Foraging habitat)	#	2.64	0–6
	Canopy (F)	#	12.36	4–21
	Understory (F)	#	2.08	0–8
	Ground (F)	#	2.61	0–11
	STAND STRUCTURE	Stand density (N)	Stems·ha ⁻¹	724.6
Basal area		m ² ha ⁻¹	32.4	2.4–82.6
Quadratic mean diameter (QMD)		cm	22.9	10.7–35.6
Dominant height (Ho)		m	13.9	7.0–19.1
Snags		snags·ha ⁻¹	80.1	0.0–647.2
Cavities (Cavit)		cavities·ha ⁻¹	16.6	0.0–85.0
Herbaceous cover		%	54.9	10.0–90.0
Shrub cover (Shrub)		%	43.6	2.0–100.0
Proportion of thick wood ^a		%	34.7	0.0–81.7
Variability in diameter size ^b			184.1	17.9–570.2

^a Proportion of thick wood refers to the percentage of the total basal area of the plot that corresponds to trees with Diameter at Breast Height (DBH) > 32.5 cm.

^b Variability in diameter size refers to the SD of stand density (stems/ha) that respectively corresponds to three classifications of wood depending on DBH. The three wood classes are ‘thin’ (7.5 ≤ DBH < 22.5 cm), ‘medium’ (22.5 ≤ DBH < 32.5 cm) and ‘thick’ (DBH ≥ 32.5 cm). This classification is based on the typical characteristics of mountain pine in the Pyrenees (Coll et al., 2012).

Appendix A). Specialists were those species living exclusively or predominantly in forests, and generally avoiding non-forested covers, whereas generalists were species that can breed in the forest but also use shrubby or other open habitats with trees (Gil-Tena et al., 2009). Ubiquitous birds can breed and forage in a wide range of habitats, like shrubs, pastures and crops, and also sometimes in forests, especially in open forests. Classification based on nest location (i.e. cavity, canopy, understory, ground nesters) and foraging behavior (i.e. trunk, canopy, understory, ground foragers) was supported by local literature (Muntaner et al., 1983; Estrada et al., 2004) and general references (Cramp and Perrins, 1993).

2.3. Forest stand descriptors

For each bird point-count, we sampled forest stand variables in three 10 m radius plots, one at the centre of the point-count and the other two 50 m eastwards and westwards. At each plot, we measured several stand descriptors including stand density, basal area, quadratic mean diameter, dominant height, total number of snags (i.e. standing dead trees) and cavities per hectare, percentage of thick wood, variability in tree diameter size and percentage of non-tree-vegetation ground cover (see Table 1 for summary statistics and definitions of the variables). Stand variables were determined as average of the three plots. Basal area was calculated based on 5-cm diameter classes, whereas dominant height was the average height of the two thickest

stems in each forest plot. Percentage of vegetation cover was measured separately for herbaceous and shrub cover (vegetation height < 25 cm and > 25 cm, respectively; see Table 1). Cavities were recorded at five 200-m transects separated by 30 m running through the point-count survey.

2.4. Analyses

2.4.1. Bird abundance across management stages

Given the point-count nature of our data, we used the non-parametric Kruskal-Wallis test to assess differences in bird abundance across management stages, using abundance of each bird guild as response variable and management stage as independent variable (with four levels: unmanaged, after preparatory cuts, after regeneration cuts, and after removal cuts). We then performed pairwise post-hoc comparisons among management stages using the Nemenyi test for multiple comparisons.

2.4.2. A likelihood approach to model bird abundance as a function of forest structure

We used likelihood methods and model selection to analyze the effect of forest structure on bird abundance. This analytical framework allows to identify and select among competing alternative models, in contrast to the traditional frequentist approach of rejecting a single “null” hypothesis (Burnham and Anderson, 2002; Canham and Uriarte, 2006). Following the principles of likelihood estimation, we estimated model parameters that maximized the likelihood of observing the abundance data measured in the field given a suite of alternative models. In contrast to *p*-values, likelihoods can be calculated for a set of alternative models and provide an explicit measure of the strength of evidence for any particular model or parameter value (Canham and Uriarte, 2006).

From the set of forest stand descriptors, we selected a subset that summarized different forest features that can have an effect on bird abundance, can be affected by management, and are easy to measure, avoiding at the same time selecting pairs of strongly correlated variables (Spearman $\rho > |0.6|$) (see Table A2 in the Appendix A). The final set of selected potential predictors of bird guild abundance included stand density, quadratic mean diameter, dominant height, number of cavities, and percentage of shrub cover (Table 1). We did not include basal area and number of snags due to high correlations with stand density, or proportion of thick wood and variability in diameter size due to their high correspondence with quadratic mean diameter. Herbaceous cover was not considered in the final analyses as they showed poor overall explanatory capacity in preliminary analyses using univariate models (Table A3).

We conducted separate analyses for the abundance of each bird assemblage defined in the previous section. Following an approach similar to that used in several tree growth studies (Canham and Uriarte, 2006; Gómez-Aparicio et al., 2011), we defined a *full model* in which abundance for each bird guild was modelled as function of several multiplicative components: (1) potential abundance, i.e. estimated abundance when all the other factors (i.e. predictors) are at optimal values, and a set of scalar modifiers that quantified the effects on bird abundance of the subset of selected predictors: (2) stem density, (3) quadratic mean diameter, (4) stand dominant height, (5) number of cavities per hectare, and (6) shrub cover. Our full model was thus estimated as:

$$\begin{aligned} \text{Observed Abundance} &= \text{Potential Abundance} * \text{Density Effect} \\ &* \text{Diameter Effect} * \text{Height effect} * \text{Cavities Effect} \\ &* \text{Shrub effect} \end{aligned} \quad (1)$$

where density effect, diameter effect, height effect, cavities effect and shrub effect are all factors that range from 0 and 1, and thus act to reduce the estimated potential abundance. It is worth to remind that

potential abundance is one of the parameters estimated by the model, and indicates the estimated abundance when all the other factors are at optimal values. In other words, when stand density, quadratic mean diameter, dominant height, number of cavities and shrub cover are all at the levels that maximize bird abundance (i.e. when their effects equal 1), then observed abundance equals the estimated potential abundance.

Each of the reducing factors (density effect, diameter effect, dominant height effect, cavities effect and shrub effect) were estimated using a bivariate Gaussian function, which serves to detect non-linear effects of the predictor on the response variable. The formulation of the diameter effect is shown below for demonstrative purposes, but each term was formulated in exactly the same way:

$$\text{Diameter Effect} = \exp \left[-0.5 \left(\frac{QMD - QMD_a}{QMD_b} \right)^2 \right] \quad (2)$$

where *QMD* is the stand quadratic mean diameter (in cm) and *QMD_a* and *QMD_b* are estimated parameters. *QMD_a* is the quadratic mean diameter at which maximum potential abundance occurs, and *QMD_b* controls the breadth of the function (i.e. variance of the Gaussian distribution). This equation usually produces the classic Gaussian distribution but can also produce sigmoidal, monotonic curves within restricted ranges of either axis.

2.4.3. Parameter estimation and model selection

Model selection was performed via the corrected Akaike Information Criterion (AICc), with lower AICc values indicating stronger empirical support (Burnham and Anderson, 2002). In this sense, two models were considered to have similar empirical support when $\Delta\text{AICc} < 2$. Following Arnold (2010), we fit the full model that included all the candidate explanatory variables (see Eq. (1)), and we compared its AICc with a set of alternative models in which we sequentially eliminated variables. Following the principle of parsimony, if eliminating a variable did not worsen substantially the empirical support for the model (i.e. $\Delta\text{AICc} < 2$), we discarded the higher order model. We sequentially eliminated variables until no additional covariate could be eliminated without leading to a substantial increase in AICc. The list of selected variables for each bird guild can be found in Table 2, and the AICc of all the alternative models is in Table A3 in the Appendix A. The most likely parameters were estimated through simulated annealing, a global optimization procedure, and models were constructed assuming a Poisson distribution of error term, as the dependent variables were count data. R^2 of the relationship between observed and predicted abundance was used as a measure of goodness-of-fit. All analyses were performed using the R statistical software (R Development Core Team, 2014).

3. Results

3.1. Variation of bird guild abundance in mountain pine forests

A total of 33 different bird species were recorded (species richness = 9.7 ± 2.6 , mean \pm SD), with an average bird abundance per plot of 19.7 ± 4.4 individuals. All bird guilds considered presented a wide range of abundance values, being scarce or even absent in some surveyed stands (Table 1). On average, the mountain pine forests surveyed had a higher abundance of forest specialists (mean = 11.2 individuals) than generalists (mean = 8.1), and held few ubiquitous species (mean = 0.4, Table 1). In terms of nesting habitat, the most abundant guilds were those nesting in cavities and in the canopy (mean = 8.8 and 7.1, respectively), whereas comparatively few birds were understory or ground nesters (mean = 2.5 and 1.3, respectively). Canopy foragers were the most abundant foraging guild (mean = 12.4), and far fewer birds foraged in the trunk, ground or understory (mean = 2.6, 2.6 and 2.1, respectively).

Table 2

Explanatory variables included in the selected model for each bird guild, number of parameters (NP), and R^2 of the relationship between observed and predicted abundance. A comparison of the AICc of all the fitted models can be found in Table A3 in the Appendix A.

	Stand density	Quadratic mean diameter	Dominant height	Cavities	Shrub cover	NP	R^2
<i>Habitat breadth</i>							
Total	✓	✓	✓	✓	✓	12	0.24
Specialists	✓	✓	✓	✓	✓	10	0.42
Generalists	✓	✓	✓	✓	✓	12	0.21
Ubiquitous	✓		✓			6	0.42
<i>Nesting habitat</i>							
Canopy nesters	✓		✓	✓		8	0.15
Cavity nesters	✓	✓	✓	✓	✓	12	0.35
Understory nesters	✓	✓	✓		✓	10	0.11
Ground nesters	✓	✓		✓		8	0.43
<i>Foraging habitat</i>							
Canopy foragers	✓		✓		✓	8	0.20
Trunk foragers			✓			4	0.40
Understory foragers		✓	✓		✓	8	0.07
Ground foragers	✓	✓		✓		8	0.15

3.2. Bird guild abundance across management stages

Total bird abundance was maximum after regeneration cuts, whereas there were no significant differences between the other two management stages and unmanaged forests (Fig. 2). In this sense, regeneration cuts favoured canopy nesters and canopy foragers (Figs. A1 and A2 in the Appendix A), (Table 1). For most bird guilds, unmanaged forests showed similar abundance to managed forests, with the exception of specialists, cavity nesters and trunk foragers whose numbers dropped significantly after the removal cuts (Figs. 2, A1 and A2). However, this decrease was offset by the high numbers of generalists, ubiquitous, ground nesters and ground foragers that were found after the removal cuts, so net total bird abundance was similar.

3.3. Bird guild response to forest stand descriptors

The fitted models explained between 7% (understory foragers) and 43% (ground nesters) of the observed variation in bird abundance, with strong variability across guilds. Models for specialists, ubiquitous, cavity nesters, ground nesters and trunk foragers had comparatively high explanatory power ($R^2 \approx 0.4$; Table 2). Models for ground foragers had considerably lower explanatory power than for ground nesters ($R^2 = 0.15$ and 0.42 , respectively; Table 2). The full model reached the strongest empirical support for three guilds (total species, generalists and cavity nesters). However, in other cases simpler models were chosen as they had equivalent or stronger empirical support to the full model (Table 2).

Dominant height and stand density emerged as the strongest predictors of bird abundance, as indicated by the number of selected models in which these variables were present (Table 2). Most bird guilds responded positively to dominant height and decreased monotonically in abundance with increasing stand density (Figs. 3–5). The decrease in abundance with stand density was particularly sharp for ubiquitous, but also for ground nesters and ground foragers, whereas forest specialists and cavity nesters were less responsive to this variable (Figs. 3 and 4). Contrary to the rest of the guilds, ubiquitous species

showed an unimodal response to dominant height, reaching a peak at 10 m (Fig. 3). Specialists and cavity nesters positively responded to quadratic mean diameter, whereas generalists, understory nesters and foragers, ground nesters and foragers and total abundance were negatively associated (Figs. 3–5).

Cavities and shrub cover were the least influential variable across guilds, although they were predictors of bird abundance for some guilds (Table 2). Abundance of cavity nesters increased with the number of cavities (Fig. 4), whereas response of ground nesters and foragers varied with number of cavities in an unimodal way, peaking at between 10 and 15 cavities per hectare (Figs. 4 and 5). In the case of ground nesters this seems to obey to intrinsic characteristics of a few stands after removal cuts. Shrub cover was a good predictor for understory nesters and foragers (Table 2 and Figs. 4 and 5). These two guilds—as well as, in a lesser extent, generalists—responded positively to shrub cover, whereas specialists, cavity nesters and canopy foragers responded negatively to it (Figs. 3–5).

4. Discussion

4.1. Effect of shelterwood system on bird communities of mountain pine forests

Our results find that unmanaged mountain pine stands do not harbour higher bird abundances than forests managed under a shelterwood system, as already observed elsewhere (Goodale et al., 2009; Duguid et al., 2016). In this sense, it is important to note that despite the lack of forest management for decades, unmanaged stands in the region are not necessarily in old-growth stages. Many mountain pine forests in the Pyrenees are relatively young and thrive on ancient crop or pasture lands, so they are still heavily conditioned by land-use legacies (Ameztegui et al., 2016). Forest structures developed in unmanaged mountain pine forests do not necessarily encompass enough habitat heterogeneity unless natural disturbances occur. In such dense homogeneous stands, there is no promotion of canopy development, so they do not harbour more canopy foragers and nesters—which are some of the most abundant guilds in the mountain pine bird community—than managed stands. However, cavity nesters may continue to proliferate in unmanaged stands due to increased cavity and snag availability (but see Mahon et al., 2008 for contrasted responses depending on species). Given the particular conditions and history of unmanaged forests in the region, it may be that with longer periods under natural dynamics, unmanaged mountain pine forests could harbour richer bird communities than observed here.

In agreement with previous studies, general stand descriptors such as stand density, quadratic mean diameter and dominant height were the most influential variables, whereas the association of bird abundance with shrub cover and cavities was less influential and guild-specific (Camprodon et al., 2008; Nikolov, 2009; Balestrieri et al., 2015; Mag and Ódor, 2015). Although the response of bird guild abundance to quadratic mean diameter was often similar to stand density but weaker, some bird guilds showed intrinsic patterns of response to stand density and dominant height (see Figs. A3–A5 in the Appendix A). Abundance of specialists and cavity nesters peaked with increasing dominant height at intermediate stand densities whereas generalists, canopy nesters and foragers and understory nesters responded positively to dominant height but negatively to increasing stand density, and trunk foragers increased with dominant height regardless stand density. This positive response to dominant height and uneven to different levels of stand density agrees with the preference of many forest guilds for mature and heterogeneous stands (Nikolov, 2009; Bergner et al., 2015). On the other hand, ground nesters and foragers showed a negative response to stand density regardless dominant height according to their predominant ubiquitous behavior.

As expected, cavity availability increased cavity nesters' abundance. In addition, number of cavities per hectare was strongly correlated with

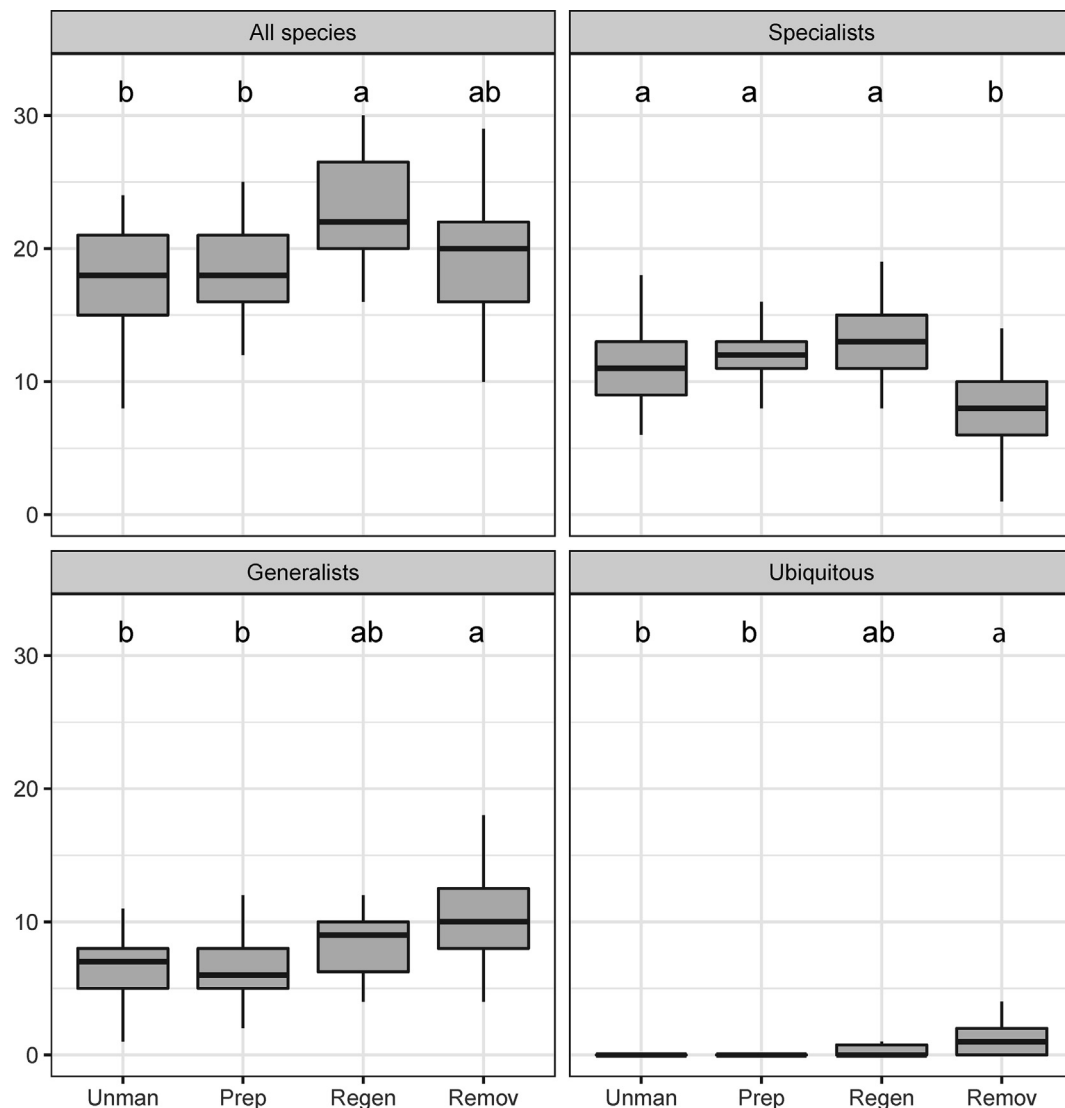


Fig. 2. Differences in observed bird guild-specific abundance based on habitat breadth in *Pinus uncinata* forests in the Pyrenees across management stages. Differences were based on a non-parametric Kruskal-Wallis test. Stages with the same letter indicate non-significant differences according to Nemenyi tests for multiple comparisons ($p > .05$). *Unman*: unmanaged forests; *Prep*: after preparatory cuts; *Regen*: after regeneration cuts; *Remov*: after removal cuts. Lower and upper whiskers indicate the 5% and 95% quartiles of bird abundance, lower and upper hinges indicate the first and third quartile, and the central black line indicates the median value.

abundance of snags (Spearman's rho = 0.53; Table A2), which provide numerous nesting sites for cavity nesters as well as a supply of feed substrates (i.e. invertebrates) for trunk foragers such as woodpeckers (Mahon et al., 2008; Nikolov, 2009; Camprodon et al., 2015; Mag and Ódor, 2015). Shrub cover also explained a part of the abundance of understory nesters and foragers, positively influencing them in agreement with previous research (Camprodon and Brotons, 2006; Bergner et al., 2015; see references in Mag and Ódor, 2015).

The reduction of stand density in mountain pine forests after regeneration cuts increased the abundance of common breeding birds, as hypothesized. Both canopy nesters and canopy foragers responded positively to regeneration cuts, since they found adequate nesting and foraging substrates in those conditions. Nevertheless, the moderate explanatory power of the most supported models for these two guilds ($R^2 \leq 0.2$) reflected that the considered stand variables were not predicting all the abundance variability. Stand structure after regeneration cuts (lower stand density with still relatively high dominant height) probably offered a greater diversity of habitat structures than excessively dense stands. The moderate reduction in stand tree density after those cuts can favour canopy development and therefore proportionate habitat for guilds such as canopy nesters and foragers (Goodale

et al., 2009; Balestrieri et al., 2015), whereas the remaining seed trees (usually the biggest ones, with well-developed crowns) and snags allow to keep stable or even increase the abundance of cavity nesters and trunk foragers (Goodale et al., 2009; Balestrieri et al., 2015; Duguid et al., 2016). Taller trees in late-successional Macedonian pine forests in Bulgaria positively correlated with canopy foragers, which may be explained by their larger vertical canopy volume and higher arthropod availability (Nikolov, 2009). Moreover, less dense stand structures after regeneration cuts can allow shrub development (Coll et al., 2011) and provide habitat for early-successional guilds nesting and foraging in the understory, keeping their populations stable even after the final cuts. However, we cannot rule out that increased light availability after regeneration cuts could also enhance shrub species richness, which may also contribute to increase understory nesting and foraging bird abundance in mountain pine forests (e.g. blueberries; Montaner et al., 2016). In this sense, model explanatory power was the lowest for both guilds ($R^2 \leq 0.11$).

In opposition to the positive effect of regeneration cuts on many bird guilds, the open habitat conditions created after removal cuts can negatively affect forest specialists, cavity nesters and trunk foragers, unless enough large trees are retained. Nevertheless, they did favour

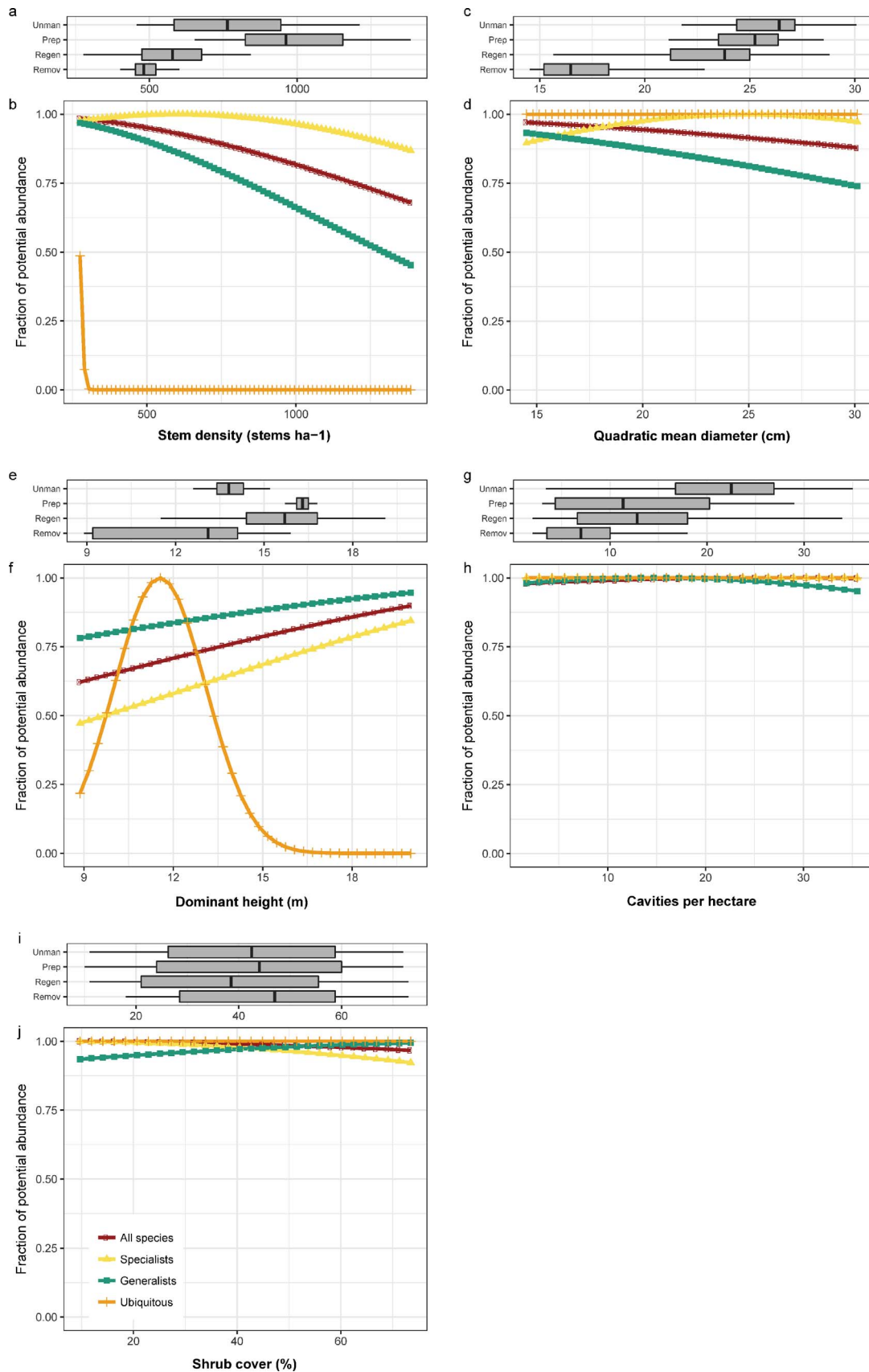


Fig. 3. Distribution of the main forest structural features across management stages (a, c, e, g, i) and effect of structural features on bird guild-specific abundance based on habitat breadth in *Pinus uncinata* forests in the Pyrenees (b, d, f, h, j). The effect of each variable is calculated for mean conditions for the rest of the variables. See Table A4 in the Appendix A for the estimated parameters of the corresponding functions. Horizontal lines at $y = 1$ indicate lack of effect of the predictive variable for that guild, and are shown for comparative purposes. *Note that the response of all species and specialists to number of cavities overlaps with that of specialists and is thus not visible. *Unman*: unmanaged forests; *Prep*: after preparatory cuts; *Regen*: after regeneration cuts; *Remov*: after removal cuts.

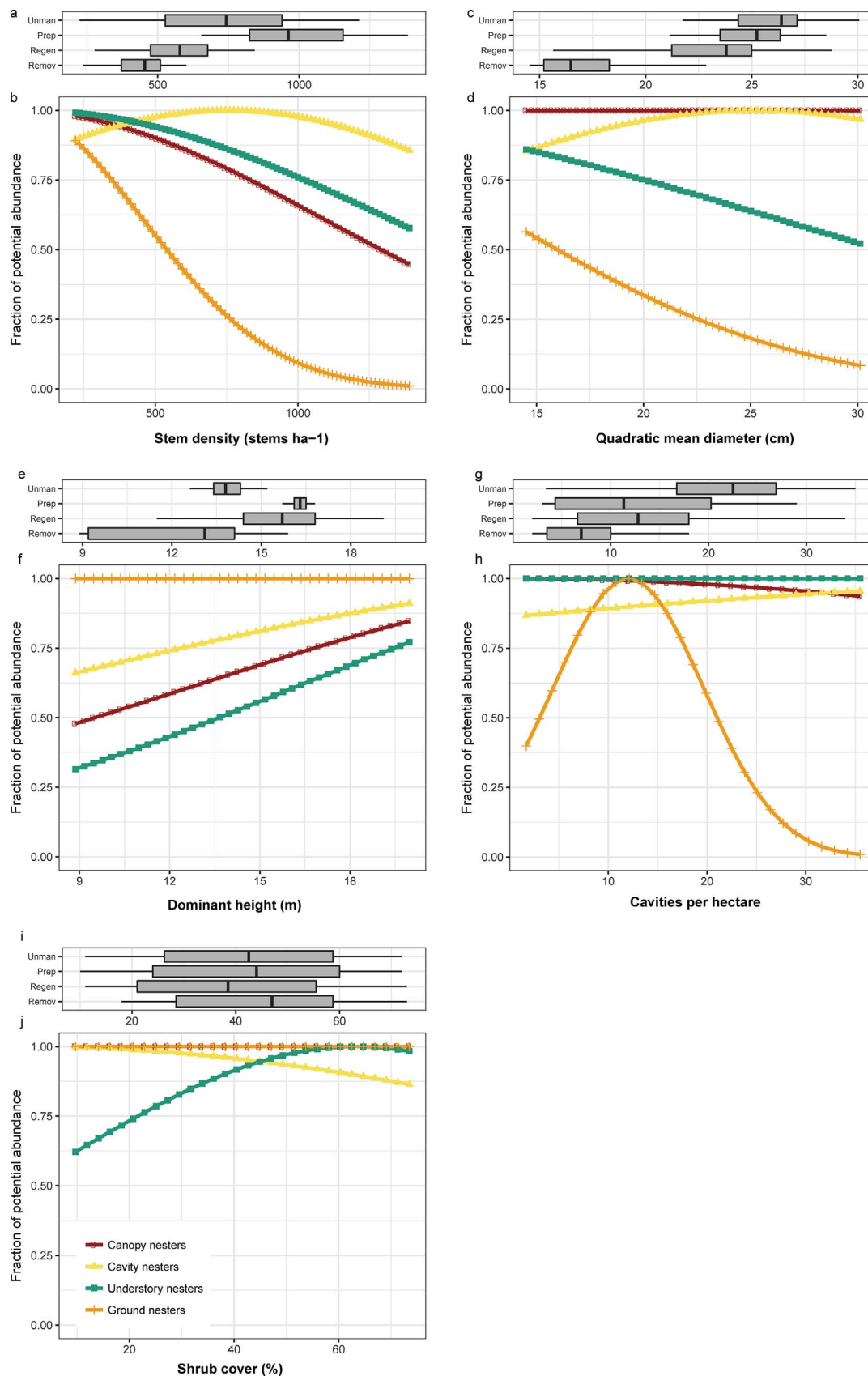


Fig. 4. Distribution of the main forest structural features across management stages (a, c, e, g, i) and effect of structural features on bird guild-specific abundance based on nesting habitat in *Pinus uncinata* forests in the Pyrenees (b, d, f, h, j). The effect of each variable is calculated for mean conditions for the rest of the variables. See Table A4 in the Appendix A for the estimated parameters of the corresponding functions. Horizontal lines indicate lack of effect of the predictive variable for that guild, and are shown for comparative purposes. *Note that the response of canopy nesters to shrub cover overlaps with that of ground nesters and is thus not visible. *Unman*: unmanaged forests; *Prep*: after preparatory cuts; *Regen*: after regeneration cuts; *Remov*: after removal cuts.

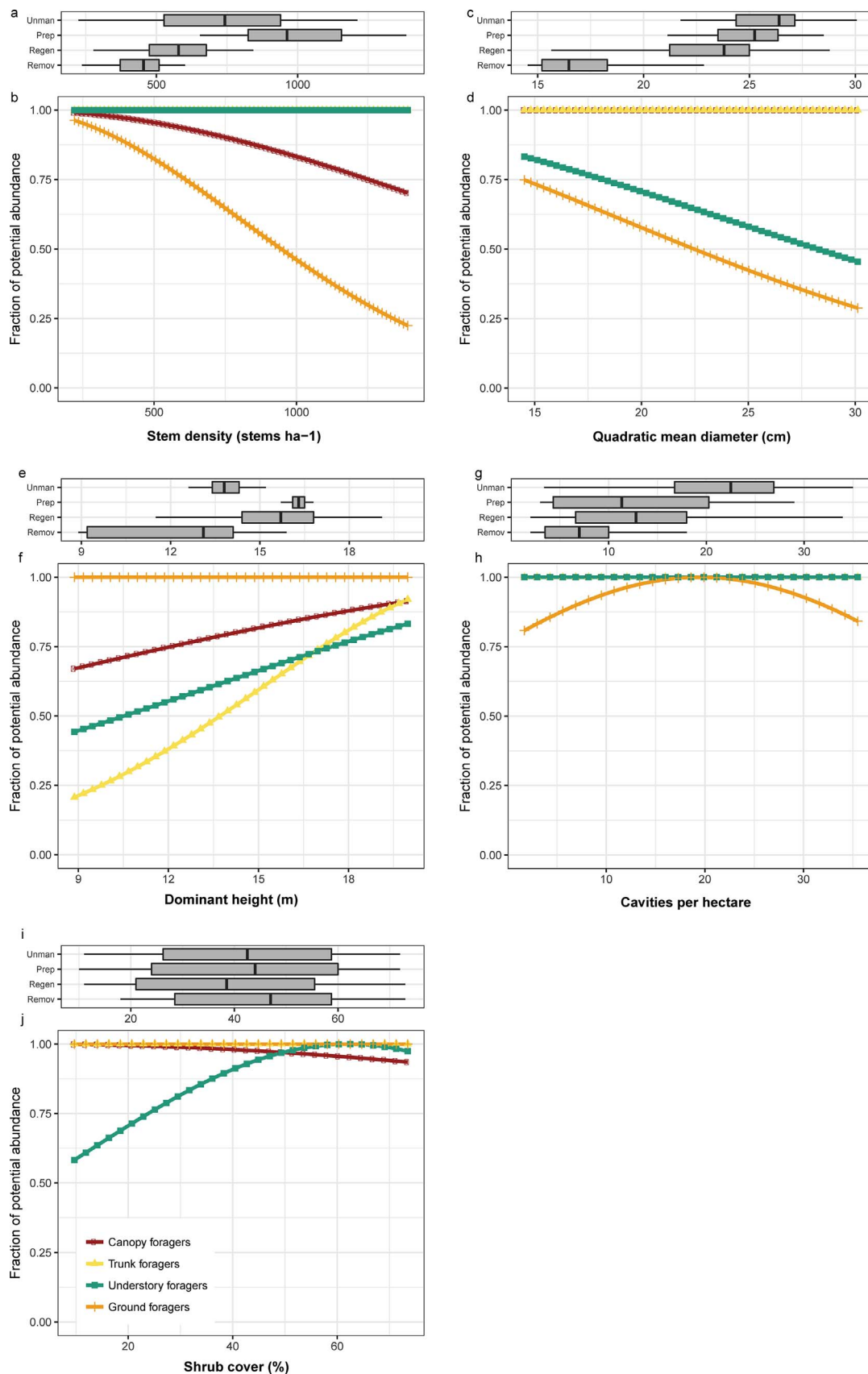


Fig. 5. Distribution of the main forest structural features across management stages (a, c, e, g, i) and effect of structural features on bird guild-specific abundance based on foraging habitat in *Pinus uncinata* forests in the Pyrenees (b, d, f, h, j). The effect of each variable is calculated for mean conditions for the rest of the variables. See Table A4 in the Appendix A for the estimated parameters of the corresponding functions. Horizontal lines indicate lack of effect of the predictive variable for that guild, and are shown for comparative purposes. *Note that the response of trunk foragers to stem density, quadratic mean diameter, cavities per hectare and shrub cover overlap with that of understory foragers, canopy foragers and ground foragers, respectively, and are thus not visible. *Unman*: unmanaged forests; *Prep*: after preparatory cuts; *Regen*: after regeneration cuts; *Remov*: after removal cuts.

ubiquitous species, ground nesters and ground foragers, which tend to be less dependent on forest structures (Duguid et al., 2016). Some of these species have experienced strong population declines in the last few decades due to the widespread expansion of forest and increasing scarcity of open shrubby habitats at landscape scales (Estrada et al., 2004). In the absence of natural disturbances, shelterwood system may thus be a potential tool to enhance biodiversity conservation for open-habitat species after widespread afforestation, as already suggested in other regions with similar constraints, like New England (Goodale et al., 2009; Duguid et al., 2016). Nevertheless, these positive effects of removal cuts on open-habitat birds remain transient (i.e. around one or two decades until canopy closure), and if these species are to be promoted, then spatio-temporal planning policy needs to target enough heterogeneity at landscape scale according to the regional species pool.

4.2. Implications for forest management

Our results indicate that shelterwood management can maintain or even promote the total abundance of common bird guilds in mountain pine forests, in comparison with the typical continuous stands resulting from afforestation after drastic land-use changes like those seen during the 20th century in the Pyrenees. An increase in bird abundance was observed in stand structures typically occurring during most of the regeneration period, only to decrease after the removal cuts. Remarkably, abundant bird guilds such as canopy foragers and nesters were favored by the stand structure resulting after regeneration cuts. Nevertheless, the impacts of removal cuts on forest specialists are not negligible, and could be minimized by retaining some structural legacies that are key for several bird guilds. For instance, attention should be paid to keeping a sufficiently high availability of cavities throughout the regeneration period, even after the last removal cuts when number of cavities usually drops. In our study, maximum bird abundance was reached when cuts left 10–20 cavities, i.e. the values observed mostly after regeneration cuts. In this sense, any snag naturally occurring in the forest should be retained, and large trees with cavities should be preferentially kept after regeneration and removal cuts to achieve similar cavity availability.

The presence of large, tall trees—even at low total stand densities—was also shown to be important for several bird guilds, particularly forest specialists, cavity nesters and trunk foragers. Therefore, during the removal cuts, some trees could be left uncut for a longer time than just the regeneration period. This method has been called “irregular shelterwood” or “shelterwood with reserves” (Smith et al., 1997), where reserves can include snags or living trees of various sizes and classes that provide supplementary habitat and food (Duguid et al., 2016). Retention forestry has been applied worldwide during the last three decades due to its multifunctional role but more insights are needed into the applicable retention thresholds, specifically concerning the study area (Gustafsson et al., 2012). We believe that when possible, these structural legacies should be retained at least until the next preparatory thinning so as to ensure their continuous presence until the development of the next cohort, and should be protected against windthrow and snow – the main disturbances in the Pyrenees – by some accompanying trees.

Considering functional bird guilds based on different life traits beyond habitat breadth (i.e. nesting habitat and foraging habitat) allowed us to determine many guild-specific responses to the different forest structural features and to strength our inferences. Moreover, our recommendations encompass common breeding bird communities, not necessarily rare or endangered species in the Pyrenees such as Capercaillie and Tengmalm’s owl that require large areas of continuous forest cover (Mariné and Dalmau, 2000; Estrada et al., 2004; Ménoni et al., 2012; Villero et al., 2015). Previous studies propose that these endangered species, despite requiring continuous forest cover, can adapt to some degree of forest management if it keeps corridors or patches of mature forest with heterogeneous understory (Ménoni et al.,

2012). These corridors can be achieved by silvicultural methods that maintain a continuous forest cover, such as group selection, or by leaving some patches of forest unmanaged in the most critical areas.

Forest planning at landscape scale has previously been advocated as a means to enhance forest bird communities (Gil-Tena et al., 2007), and has recently started to be applied in the study area. The best strategy to foster avian diversity at landscape level could consist of combining a mosaic of managed and unmanaged patches at different development stages (Goodale et al., 2009; Balestrieri et al., 2015; Mag and Ódor, 2015; Duguid et al., 2016). The average patch size of natural disturbances in the region (mainly snow and wind storms), although highly variable, is around 17 hectares (Martín-Alcón and Coll, 2008), and could be taken as a starting point in landscape management. However, there is still a need for more insight to determine the optimal patch size and distribution in the landscape to promote avian diversity while ensuring the preservation of endangered species or other forest ecosystem services (Gustafsson et al., 2012). In this sense, complementary measures may also be implemented at landscape scale, such as forest stewardship promoted by agreements between forest owners and NGOs or private foundations, or by the establishment of forest networks in which the recovery of naturalness and/or the promotion of biodiversity are seen as assets.

4.3. Conclusions

We observed that a shelterwood system can prove an adequate management tool to break the homogeneity of mountain pine forests at stand level and thus promote the abundance of most common bird guilds. In a shelterwood system, different stand structures are created throughout the regeneration period (30–40 years in the study area), with contrasting effects on the abundance of bird guilds. Here, maximum total bird abundance was observed after the regeneration cuts, when stand density is reduced but there are still substantial amounts of standing large, mature trees and cavities available. By obtaining quantitative relationships between the main structural features affected by tree harvests and the abundance of birds, we reinforced our biodiversity conservation guidelines for mountain pine forests in the Pyrenees, and generated management recommendations that are valid for forests managed not only by a shelterwood system but also by other silvicultural methods.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.09.002>.

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