Effects of undergrowth clearing on the bird communities of the Northwestern Mediterranean Coppice Holm oak forests

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Abstract

Undergrowth clearing is a widespread forest management technique used in many Mediterranean regions to reduce dense vegetation in order to prevent fire or to facilitate other forest exploitation activities. Here, we analyze the effects of undergrowth clearing on biodiversity by focusing on the variations in bird diversity in Holm oak forests in Catalonia (north-east Iberian Peninsula) under different forest management regimes: (1) coppice Holm oak forests where the undergrowth layer has been completely cleared, (2) partially cleared forests and (3) cleared and tree thinned forests and finally, (4) undisturbed forests. The synchronic comparison approach was used in conjunction with a before–after control impact (BACI) experiment in which the effects of undergrowth clearing were explicitly measured. Complete undergrowth clearing resulted in the almost complete disappearance of three Warbler species (Subalpine Warbler, Sardinian Warbler and Garden Warbler). Partial clearing also led to a marked reduction in the numbers of these three species, but the presence of Sardinian and Garden Warblers was maintained in the treated forests. Complete undergrowth clearing accompanied by tree thinning also led to a decrease in amount of undergrowth species and involved additional negative effects for species such as Wren, Robin, Blackbird and Blackcap. Only one species, the Nightjar, appeared to benefit from undergrowth clearing, while many others increased their numbers only when clearing was applied together with tree thinning: Turtle dove, Mistle thrush and Cirl bunting. Undergrowth clearing brought about a significant simplification in the vertical structure of the forest, which probably reduced foraging opportunities and breeding resources for most undergrowth species. These effects became more pronounced when tree thinning was applied together with undergrowth clearing. To reconcile forest management and bird diversity, undergrowth clearing should be applied selectively to ensure that a certain number of undergrowth patches, preferably corresponding to different shrub species, are not affected by management treatments.

Keywords: Clearing; Undergrowth vegetation; Quercus ilex; Birds; Thinning; Forestry

1. Introduction

Mediterranean forests have traditionally been subject to strong human pressure through activities such as forestry, coal production or vegetation clearing (Blondel and Aronson, 1999). However, recent socioeconomic changes in some Mediterranean regions have induced a reduction of most of these activities typically leading to an accumulation of vegetation, especially in the shrub and lianas layers of the undergrowth. In this context, undergrowth clearings are currently the main management activity effecting forests in many regions particularly in the north-western Mediterranean basin. Mechanical undergrowth clearing aims to reduce the densely developed shrub and liana vegetation layers and are mainly used to eliminate the combustible load but also to control tree competition and favour sapling regeneration or access to the forest (Garolera, 1991; CPF, 1992; Mesón and Montoya, 1993). The increase in the number and impact of forest fires during recent decades (Terradas, 1996) has boosted the use of undergrowth clearing, although, the effectiveness of this forestry technique to fight the spread of fire has been questioned because of its low cost effectiveness (Camprodon, 2001).

Although the influence of forestry, fire or grass management on biological diversity in the Mediterranean scrubs, garrigues and maquis has been studied (Blondel, 1981; Prodon, 1988; Pons, 1998), the effects of undergrowth clearing have been...
largely neglected and are not currently used in the criterion which guides forest management in the region. Clearing is likely to have a strong impact on biodiversity, since it entails a significant elimination of forest biomass. In Mediterranean forests, more than 40% of the total floristic richness, as quantified by forest plants, is located in the shrub layer. Furthermore, most of the arthropod biomass inhabiting Holm oak forest, essential for the undergrowth feeding of diverse faunal groups, also occurs in the shrub undergrowth (pers. obs.). Vegetable biomass is often a good indicator of the density and specific bird composition of forest habitats (MacArthur, 1964; Wilson, 1974; Levin, 1976; Prodon and Lebreton, 1981; James and Wamer, 1982). In particular, a recurrent positive relation between bird richness, density and extension of the undergrowth layer has been found (for example, Prodon and Lebreton, 1981; Canterbury and Blockstein, 1997; Donald et al., 1997; Díaz et al., 1998). Crawford et al. (1981) concluded that the crown cover and the height of the undergrowth layer were the most important factors in explaining the distribution of forest passerines. These studies linking undergrowth vegetation and bird communities suggest that an intense modification of the shrub layer either by mechanical means, grass or prescribed burning, may have a significant impact on bird fauna. In fact, the situation after a total clearing of the undergrowth can be compared to one after a forest fire in which trophic availability and nest site availability are limited, forcing territorial birds to breed in unusual locations, consequently increasing their exposure to predation or reducing their food supply (Renwald, 1977; Wright, 1981; Winter and Best, 1985; Petersen and Best, 1987). In spite of these predicted effects, coppice regeneration may favour rapid nest establishment even before the development of a more dense vegetation layer by growth of new seeds (Brooker and Rowley, 1995; Pons, 1996). However, unlike burning, clearing of the undergrowth does not affect tree canopies and therefore, undergrowth recovery tends to be slower unless clearing is accompanied by tree thinning.

The objective of this study is to determine the association between forest birds and the structure of the shrub layer in Mediterranean forests and test the hypothesis that undergrowth clearing has a strong impact on the occurrence of forest birds, especially those known to rely on low vegetation layers. Furthermore, we explored the combined impact of undergrowth clearing with other forestry practices (i.e. tree thinning) on the bird community. We conclude by suggesting some recommended guidelines aimed at making forest management compatible with the conservation of species associated with Mediterranean shrubby vegetation.

2. Methods

2.1. Study area

The study area, of about 2000 km², is located in the Catalan Pre-littoral System (north-east Iberian Peninsula). It has a relatively rainy coastal climate with a short cool winter (de Bolòs, 2001). Coppice Holm oak forests (Viburno-Quercetum ilicis) are dominant in most mountain areas up to 1400–1500 m. The arboreal layer of coppice Holm oak forests is rather short and the trees never reach a great size: 8.5 m average maximum height, 12.4 cm average diameter at breast height (dbh), with few trees reaching 35 cm dbh. Due to their limited size, trees encounter strong competition for light and soil resources from the well developed ligneous undergrowth which is dominated by shrubs such as the Strawberry tree (Arbutus unedo), Laurustinus (Viburnum tinus), Heather (Erica multiflora), Lentiscus (Pistacia lentiscus) and Rockrose (Cistus salviifolius) and lianas such as Bindweed (Smilax aspera), Ivy (Hedera helix) and Bramble (Rubus ulmifolius). Sprouts of Holm oak may also appear in the coppice forest undergrowth. The arboreal layer, with close crown contact, is dominated by the Holm Oak (Quercus ilex), accompanied in some areas by Evergreen oak (Quercus humilis), Cork oak (Quercus suber) or more occasionally Aleppo pine (Pinus halepensis).

The main forest management technique applied to Holm oak forests in the area is sprout selection. This technique reduces the number of sprouts per tree leaving from between two to four stumps. These are eventually harvested for firewood once they reach between 18 and 25 cm dbh (Garolera, 1991; CPF, 1992). Cut rotation time ranges from 10 to 15 years. Usually, before a sprout selection, the undergrowth layer is cleared with a chain saw or a bush breaker. This undergrowth clearing is the main disturbance affecting the shrub layers in these Holm oak forests.

A particular case of forest management in areas used for cow pasture and ewe grass consists of undergrowth clearing applied in conjunction with the thinning of the Holm oak forest by means of strong selective cutting. These forests have a low density, open forest structure, since thinning has eliminated most stems and only the best stumps have been preserved. Overall, when taking into account the intensity and time elapsed since undergrowth management, Holm oak forests vary in the degree of cover and height of the shrub and liana layers.

When considering undergrowth structure, coppice Holm oak forests where sprout selection is the main management technique can be broadly classified a priori into four different groups (Fig. 1): (1) Coppice Holm oak forests where the undergrowth layer has been completely cleared. The entire shrub and lianas layers having been eliminated by mechanical practices. (2) Partially cleared coppice Holm oak forests which maintain approximately one-third of the shrubs and lianas. This clearing is not uniform and often clumps of shrubs and lianas may have been left behind after undergrowth clearing. (3) Cleared and thinned Coppice Holm oak forests in which all of the undergrowth is eliminated and most of the arboreal layer is filled by selective thinning. (4) Dense coppice Holm oak forest where neither clearing nor thinning have taken place. These have a high shrub and lianas cover (70–90%) and dense young growth stand.

2.2. Location of census plots

Using data from the national forest inventory, forest maps and administrative data on forest management histories in the study area (Camprodon, 2001), we selected a number of forest
tracts with a history of forest management and homogeneous vegetation structure. We classified such forest tracts into one of the four forest types described above and made sure they were uniformly distributed within the study area in order to avoid spatial biases. Within the central section of each selected forest tract, we located census plots in which the vegetation structure and the bird community was sampled. Selected forest tracts were located in forests larger than 200 ha in size, contained at least 10 ha of homogenous vegetation of the corresponding forest type and were located at least 1 km from the nearest forest tract of any other type containing a census plot. Due to the difficulty in locating adequate, large cleared, thinned forests, we located, for this forest type, up to three census plots per forest tract. In this case, census plots were located a minimum of 400 m from the nearest plot to avoid pseudo-replication (Hurlbert, 1984). All census plots were located at least 500 m from the nearest forest edge to avoid interference from surrounding non-forest habitats.

2.3. Bird census

We used point counts to estimate bird abundance at each census plot (Tellería, 1986; Bibby et al., 2000). Point counts lasted for 20 min during which all audible and visual contact was registered in three radiuses of 100 m around the central point of the census plot. All point counts were conducted within 3 h from sunrise (between 6:30 and 9:30 a.m.). Censuses were conducted between the third week of April and the last week of June during the years 1999–2002. We conducted one point count per season at each census plot. We estimated that given the long duration of the sampling (20 min), one point count per season was enough to detect most species present and therefore accurately sample different forest types. Point counts were conducted in a random order across different forest types and years of study reducing any possible temporal bias in data collection. Larger species of raptors which were occasionally observed in or around the census plots (Circus gallicus, Buteo buteo, Accipiter nisus, Strix aluco and Asio otus) were not included in the analyses.

We used species richness and abundance (number of individual contacts) per point count as variables in further analyses. We also classified bird species into different categories (Table 3) according to the patterns of micro-habitat choice as described in the literature (Muntaner et al., 1983; Snow and Perrins, 1998; Shirihai et al., 2001): trunk-foraging species (Woodpeckers, Nuthatch and Short-Toed Treecreeper), other cavity nesters (tits, genus Parus), birds using tree canopies (Wood Pigeon, Golden Oriole, Jay, Phylloscopus Warblers, Firecrest, Chaffinch and some thrushes), species of the shrub layer of the undergrowth (Wren, Robin, Blackbird and most Sylvia Warblers) and birds associated with the agro-forest open habitats (Nightjar, Turtle Dove, Serin, Greenfinch, Goldfinch, Cirl Bunting). Due to their strong dependence on the undergrowth layer, we also used another sub-guild within the shrub layer category composed only of the species of the genus Sylvia (Table 3).

2.4. Habitat inventory

We characterized vegetation structure for each forest type by a set of measurements conducted at each census plot. We described structural and floristic variables within a radius of 50 m around the central point of the corresponding census plot. The cover of different vegetation layers was visually measured at different interval heights (CV25: 0–0.25 m, CV50: 0.25–0.5 m, CV1: 0.5–1 m, CV2: 1–2 m, CV4: 2–4 m, CV8: 4–8 m,

Fig. 1. Example of study habitats in the Finestres Mountain within or adjacent to the natural park of Zona Volcànica de la Garrotxa (Catalan Pre-littoral System, NE Iberian Peninsula). Upper left, a dense Holm oak forest (DH); upper right, a partially cleared Holm oak forest (PCH); bottom left, a completely cleared Holm oak forest (CCH); and bottom right, a cleared and thinned Holm oak forest strongly felled by selective thinning (CTH).
CV16: 8–16 m), a model proposed by Prodon and Lebreton (1981). The precision of this visual method is acceptable, with the coefficient of variation estimated to be around 7% (Prodon, 1988). The cover of cleared, cut or pruned dry branches on the ground (Bran) and rock cover (Rock) were also recorded using the same method. The diameter of the trunk at breast height (dbh) was also measured for trees using diametrical classes (D) at 5 cm intervals. We grouped dbh classes into four categories: lesser trees (<D5, dbh < 2.5 cm), small trees (D5–15, dbh between 2.5 and 17.5 cm), medium sized trees (D20–30, dbh between 17.5 and 32.5 cm) and big trees (D > 30, dbh from 32.5 cm). Final variables used an expressed number of trees/ha for each of the corresponding tree size categories.

2.5. Experimental removal of the understory

To further explore the effect of undergrowth clearing on the bird community, we employed a before–after control impact approach on a section of Holm oak forest before and after undergrowth clearing management (BACI, Stewart-Oaten et al., 1986). In December–February of 1999 a complete mechanical clearing of all shrub and lianas layers in 12 ha of Holm oak forest with dense and homogenous undergrowth was carried out. This forest was located north of the study area, in the Finestres Mountain at a height of 600 m with an east-southeast aspect.

We established two controlled forest sections, one adjacent to the experimental one, and the second, of similar size, altitude, orientation and vegetable structure, located 2 km from the cleared section. Bird occurrence during the breeding season within the sections was monitored for a period of 5 years: 2 years prior to the undergrowth clearing (1997 and 1998) and 3 years following the intervention (1999–2001). The census was conducted by walking inside the forest section and locating all bird contacts on a map. We conducted 10 visits to each forest section and territories were identified on the basis of the spatial gradients are evaluated. All the census plots (n = 145), 24 bird species (excluding those with less than a total of three contacts), and 13 environmental variables were analyzed in the CCA (Table 1).

To further investigate habitat selection patterns of different guilds, we used the generalized linear model. This technique considers the dependency of discrete variables (census of birds) on a group of independent variables or indicators (i.e. habitat structure: in this case, the factors obtained by PCA). We used presence/absence of individual bird species in each census plot as a dependent variable and used logistic regressions (binomial error distribution) to evaluate species habitat relationships. In addition, we used the number of species per plot for each different guild and used Poisson error distribution to establish guild–habitat relationships. A forward step-wise procedure was applied to select significant variables only (p-level threshold p = 0.05).

Finally, changes in relative abundance of individual species after clearing treatments were evaluated using the BACI approach by applying the method of Stewart-Oaten et al. (1986). Abundances were log-transformed (ln(x + 1)), to render the residuals homoscedastic and normally distributed. For each species, the difference in (log) abundance between each treatment and the mean value of the two controls for each sampling period was calculated, and these differences were then subjected to analysis of variance of repeated measures (ANOVA). Effects were fitted for treatment (cleared-control), before/after, species and the interaction between these. Single
The cover of the understory was significantly related to forest type. In dense, reference forests, shrub cover reached, below 2 m in height, values above 50%. This cover decreased to 26–42% in partially cleared forests and to 10–27% in completely cleared forests (Table 1). Total tree density showed similar figures between different cleared forests, with abundance of sprouts, ranging between 1.750 and 2.600 trees/ha, largely within the 5–15 cm class and rarely surpassing 30 cm. On the other hand, cleared and thinned Holm oak forests had, on average, as little as 300 trees/ha, mainly within the classes 15–30 cm (Table 1). They presented an overall aspect of grazed forest, with trunks not in direct contact with the shrub and liana layers.

3. Results

3.1. Structural differences between forest types

The cover of the understory was significantly related to forest type. In dense, reference forests, shrub cover reached, below 2 m in height, values above 50%. This cover decreased to 26–42% in partially cleared forests and to 10–27% in completely cleared forests (Table 1). Total tree density showed similar figures between different cleared forests, with abundance of sprouts, ranging between 1.750 and 2.400 trees/ha, largely within the 5–15 cm class and rarely surpassing 30 cm. On the other hand, cleared and thinned Holm oak forests had, on average, as little as 300 trees/ha, mainly within the classes 15–30 cm (Table 1). They presented an overall aspect of grazed forest, with trunks not in direct contact with the shrub and liana layers.

3.2. Bird–habitat relationships and forest management

We recorded a total of 30 bird species in the Holm oak forests we analyzed. In dense forests, we detected 20 species,
whereas in totally and partially cleared Holm oak forests 18–19 species were sighted and 26 in cleared and thinned Holm oak forests. Species associated with the shrub layer were abundant in dense Holm oak forests and tended to become scarcer in forests in which the shrub layer had been reduced as a result of the undergrowth clearing management (Table 3). However, these trends varied according to the species in question. Whereas species such as the Wren and the turdids (Robin and Blackbird) appeared in cleared zones in which the arboreal layer had been unaffected by the management, Sylvia Warblers were very scarce in any type of cleared forests. For instance, the Subalpine Warbler was completely absent from totally and partially cleared forests (Table 3). The Blackcap occupied totally cleared forests, but it was significantly less abundant in dense forests (Table 3). When the clearing was accompanied by selective thinning, the Wren, the Robin and the Blackcap were less frequent and the rest of the Sylvia Warblers disappeared. Only Blackbird abundance seemed to remain relatively unchanged despite the undergrowth vegetation structure (Table 3).

Common ground foragers in the dense forests like The Wood Pigeon, the Jay and the Chaffinch, did not increase their use of forest habitats with reduced shrub cover (Table 3). Only the Chaffinch increased in abundance when the arboreal canopy

Table 3
Species abundance, total richness and abundance and richness of each guild by point count, according to the degree of undergrowth clearing or arboreal cutting

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Guild</th>
<th>DH</th>
<th>PCH</th>
<th>CCH</th>
<th>CTH</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness</td>
<td></td>
<td></td>
<td>8.30 a</td>
<td>6.36 b</td>
<td>5.44 b</td>
<td>8.60 a</td>
<td>***</td>
</tr>
<tr>
<td>Abundance</td>
<td></td>
<td></td>
<td>10.30 a</td>
<td>7.95 ab</td>
<td>6.86 b</td>
<td>9.97 a</td>
<td>***</td>
</tr>
<tr>
<td>Undergrowth species</td>
<td></td>
<td></td>
<td>5.05 a</td>
<td>2.56 b</td>
<td>1.78 c</td>
<td>1.17 c</td>
<td>***</td>
</tr>
<tr>
<td>Sylvia Warblers</td>
<td>Syl</td>
<td></td>
<td>2.80 a</td>
<td>0.82 b</td>
<td>0.22 c</td>
<td>0.03 c</td>
<td>***</td>
</tr>
<tr>
<td>Trunk-foraging species</td>
<td>Tru</td>
<td></td>
<td>0.13 b</td>
<td>0.35 b</td>
<td>0.26 b</td>
<td>1.50 a</td>
<td>***</td>
</tr>
<tr>
<td>Tits</td>
<td>Par</td>
<td></td>
<td>0.68 b</td>
<td>1.03 b</td>
<td>0.94 b</td>
<td>1.60 a</td>
<td>***</td>
</tr>
<tr>
<td>Tree-canopy species</td>
<td>Cro</td>
<td></td>
<td>2.28</td>
<td>2.15</td>
<td>2.14</td>
<td>2.07 n.s.</td>
<td></td>
</tr>
<tr>
<td>Open habitats species</td>
<td>Ope</td>
<td></td>
<td>0.17 a</td>
<td>0.21 a</td>
<td>0.28 a</td>
<td>2.07 b</td>
<td>***</td>
</tr>
<tr>
<td>Columba palumbus (Copa)</td>
<td>Wood Pigeon</td>
<td>Cro</td>
<td>0.03</td>
<td>0.21</td>
<td>0.11</td>
<td>0.13 n.s.</td>
<td></td>
</tr>
<tr>
<td>Streptopelia turtur (Sttu)</td>
<td>Turtle Dove</td>
<td>Ope</td>
<td></td>
<td></td>
<td>0.20 *</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caprimulgus europaeus (Caeu)</td>
<td>Nightjar</td>
<td>Ope</td>
<td>0.14</td>
<td>0.10</td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upupa epops (Upep)</td>
<td>Hoopoe</td>
<td>Ope</td>
<td>0.10</td>
<td>0.10</td>
<td>***</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

n        | 40 | 39 | 36 | 30

Different letters identify forest types groups according to differences in mean values of a given variable as tested by Tukey HSD or generalized linear modelling. DH: dense Holm oak forests, PCH: partially cleared Holm oak forests, CCH: completely cleared Holm oak forests, CTH: cleared and thinned Holm oak forests. n.s.: not significant.

* p < 0.05.
** p < 0.01.
*** p < 0.001.
The species acronym’s, see the text and Table 3, respectively. In order to interpret the environmental variable and variables, by means of the Monte Carlo test. Only the variables with a have been selected from a progressive evaluation of the meaning of the different Fig. 3. The relationship between the bird species and the environmental variables increased in abundance in cleared and thinned Holm oak forests, being entirely absent from dense forests. Finally, trunk-foraging species and birds from agro-forest open habitats increased in abundance in cleared and thinned Holm oak forests remaining less frequent in denser forests (Table 3).

Bird community structure in different types of forests was significantly captured by the environmental variables used. The first CCA axis, accounting for 11.2% of total variation in bird community, represented a gradient based on structural variables related to cover of shrubs and small trees (i.e. from dense to cleared forests), whereas the second gradient was positively related to tree density and negatively to rock cover (Figs. 2 and 3). The two first axes accounted for 14.9% of total variation. The presence of three shrub layer bird species, the Subalpine Warbler, the Sardinian Warbler and the Garden Warbler, which were then more abundant in dense Holm oak forests, was strongly associated to the first gradient. The rest of the shrub layer species, such as the Wren, the Robin or the Blackcap, and tree-canopy birds were associated with totally or partially cleared forests. On the other hand, birds from agro-forest open habitats, such as the Turtle Dove, the Hoopoe or the Cirl Bunting (Fig. 3), were mainly associated with cleared and thinned Holm oak forests.

Habitat selection models for undergrowth species showed a strong association of this group with PCA factors describing the low and high shrub layer and the low arboreal layer (Tables 2 and 4). Within this group of birds, the Wren and the Blackbird also selected the accumulation of dead branches on the ground (Table 4). Furthermore, we detected a negative association of the occurrence of species such as the Wren, the Blackbird and the Sardinian Warbler with the highest tree cover and also for the Wren, the Blackbird, the Blackcap and the Garden Warbler with rock cover. Trunk foraging species and tits were negatively associated with the density of small trees. Tits were the only group which had a positive association with rock cover. We did not find any significant model for tree-canopy species. Finally, birds of agro-forest open habitats tended to negatively select plots with high tree densities and dense sub-arboreal layers (Table 4).

3.3. Effects of experimental clearing on the bird community

The average cover of shrubs and lianas before the undergrowth clearing in the experimental forest section (12 ha in size) was 57% for the vegetation layers between 0.25 and 4 m. These layers were dominated by Heather, Strawberry tree, Binweed, Lentiscus, Bramble, Liguster and Old Man’s Beard. After the clearing, the average cover of these layers decreased to about 6%, before increasing progressively again to about 16% in 2002 four years after the treatment.

Before the clearing the experimental forest section hosted between 2 and 7 territories of different undergrowth bird species (Fig. 4). We found a highly significant interaction between the control-impact and the before–after factors ($F_{1,21} = 224.25, p < 0.001$) indicating that while within the control forest sections the number of occupied territories remained constant, the number of bird territories within the treatment section decreased sharply overall after the clearing of the understory (Fig. 4). We also found that the effect of the clearing was indeed species specific ($F_{6,21} = 34.18, p < 0.001$) and therefore not all species were eliminated from the plots after the undergrowth clearing (Fig. 4). During the breeding season following winter clearing, the Subalpine Warbler, the Sardinian Warbler and the Garden Warbler apparently abandoned their territories and remained absent during the years following the disturbance (1999–2001, Fig. 4). From circumstantial detection of singing males, territories of Sylvia Warblers seemed to be maintained in areas surrounding the experimental forest section and the control sections throughout these years. In contrast to other Sylvia Warblers, the Blackcap continued to use to some degree the cleared zone, but this species modified microhabitat use within the territories,
Fig. 4. Representation of temporal changes in mean number of territories within the experimental (black circles) and control forest sections (white squares) for each species commonly using the forest undergrowth: species specific contrast tests showed that the interaction between control-impact and before–after factors are significant for all species except Sylvia atricapilla, Troglodytes troglodytes and Erithacus rubecula. The arrow marks the point in time when the undergrowth clearing treatment was applied to the experimental forest section during winter 1998–1999.

Table 4
Selection of environmental variables on the undergrowth species and the different guilds, from generalized linear models, by means of the procedure of forward stepwise (whole p to enter: 0.05; whole p to remove: 0.05)

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>$\chi^2$</th>
<th>d.f.</th>
<th>%</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Undergrowth species</td>
<td>1.44 − 0.002D20–30 + 0.33 × high shrub + 0.17 × low tree + 0.20 × high tree − 0.15 × rock</td>
<td>92.51</td>
<td>5</td>
<td>47.72</td>
<td>***</td>
</tr>
<tr>
<td>Sylvia Warblers</td>
<td>−0.16 + 0.79 × high shrub + 0.28 × low tree − 0.30 × rock + 0.18 × low shrub</td>
<td>126.76</td>
<td>4</td>
<td>50.57</td>
<td>***</td>
</tr>
<tr>
<td>Trunk-foraging species</td>
<td>0.38 − 0.001D5–15</td>
<td>54.04</td>
<td>1</td>
<td>36.06</td>
<td>***</td>
</tr>
<tr>
<td>Tits</td>
<td>0.49 − 0.001D5–15 + 0.21 × rock</td>
<td>35.19</td>
<td>2</td>
<td>19.04</td>
<td>***</td>
</tr>
<tr>
<td>Open habitats species</td>
<td>0.51 − 0.01D5–15 − 0.58 × low tree − 0.33 × low shrub</td>
<td>156.86</td>
<td>1</td>
<td>63.08</td>
<td>***</td>
</tr>
<tr>
<td>Wren</td>
<td>−0.87 + 0.72 × high shrub + 0.49 × low tree − 0.67 × high tree − 0.59 × rock + 0.63 × branc</td>
<td>42.05</td>
<td>5</td>
<td>22.67</td>
<td>***</td>
</tr>
<tr>
<td>Robin</td>
<td>0.72 + CD10–15 + 1.78 × high shrub + 0.91 × high tree + 0.72 × low shrub</td>
<td>62.28</td>
<td>4</td>
<td>39.43</td>
<td>***</td>
</tr>
<tr>
<td>Blackbird</td>
<td>−1.60 + 0.001D &lt; 5 + 0.01D20–30 − 0.47 × rock + 0.39 × branc − 0.48 × high tree</td>
<td>26.54</td>
<td>5</td>
<td>13.66</td>
<td>**</td>
</tr>
<tr>
<td>Sardinian Warbler</td>
<td>2.53 + 3.06 × high shrub − 1.20 × high tree</td>
<td>97.54</td>
<td>2</td>
<td>62.71</td>
<td>***</td>
</tr>
<tr>
<td>Subalpine Warbler</td>
<td>−1.28 + 2.45 × high shrub + 0.87 × low shrub</td>
<td>86.61</td>
<td>2</td>
<td>48.66</td>
<td>***</td>
</tr>
<tr>
<td>Garden Warbler</td>
<td>−1.98 + 0.98 × high shrub − 0.74 × rock</td>
<td>23.67</td>
<td>2</td>
<td>17.75</td>
<td>***</td>
</tr>
<tr>
<td>Blackcap</td>
<td>−0.92 + 1.04 × high shrub + 0.70 × low tree + 0.65 × high tree − 0.83 × rock + 0.60 × low shrub</td>
<td>55.54</td>
<td>5</td>
<td>29.53</td>
<td>***</td>
</tr>
</tbody>
</table>

All the species follow a binominal distribution, while the guilds follow a Poisson distribution.

** $p < 0.01$.

*** $p < 0.001$. 

Fig. 4. Representation of temporal changes in mean number of territories within the experimental (black circles) and control forest sections (white squares) for each species commonly using the forest undergrowth: species specific contrast tests showed that the interaction between control-impact and before–after factors are significant for all species except Sylvia atricapilla, Troglodytes troglodytes and Erithacus rubecula. The arrow marks the point in time when the undergrowth clearing treatment was applied to the experimental forest section during winter 1998–1999.
showing a tendency to concentrate its activity along the areas neighbouring non-cleared zones. The Blackcap used the cleared zones basically for feeding and, secondarily, as singing sites, but located the nest in the non-cleared zones.

However, the distribution of Wren contacts remained basically identical before and after the clearing and occupied vegetation along small dry streams. This species took advantage of the accumulation of dead branches resulting from forest clearing and used this substrate for feeding and singing whereas it bred on the ground or rock margins. The Robin also maintained a constant use of the forest after clearing. However, more than half of the audible contacts for this species along the border of the experimental forest section corresponded to the non-cleared vegetation. Finally, the Blackbird used the cleared zones as feeding substrates by foraging on the ground. Most of the species activity also concentrated on the non-cleared parts. Nearly half of the Blackbird contacts in the cleared area corresponded to young birds. The tree-dwelling species showed no change in numbers after disturbance compared to the control.

4. Discussion

Change in perceived habitat quality is the key factor determining birds’ response to disturbances (Sousa, 1984; Wiens, 1989; Bazzaz, 1991). Prodon and Lebreton (1981) showed that as small changes in vegetal cover occur, significant impacts on the bird community may be detected when overall vegetal cover in the undergrowth is low. However, if ligneous vegetation is dense enough, clearing of the vegetation may have negligible effects on birds. In line with these predictions, the abundance of Sylvia Warblers, birds morphologically adapted to life within dense shrubs, diminished in cleared forests, but especially so when clearing of the undergrowth vegetation was almost complete. The results obtained after the experimental undergrowth clearing of a forest reinforced the trends observed in the synchronous study based on point counts regarding changes in the abundance of Sylvia Warblers following the clearing disturbance. Among this group of birds, the Subalpine Warbler appeared to be the most demanding in terms of undergrowth vegetation structure, since it prefers higher and denser shrubs and is the less arboreal of the Sylvia Warblers in the Holm oak forests, whereas the Blackcap was the most flexible species, probably due to its preferential use of tree canopies compared to other Sylvia Warblers (Fuller, 1995; Snow and Perrins, 1998; Shirihai et al., 2001). If the undergrowth clearing is accompanied by selective thinning, the combined effects of these two factors on the bird community appear more intense. This management practice diminishes the abundance of other undergrowth bird species in addition to the Sylvia Warblers, but also the thinning induces changes in the composition of the tree-canopy birds and benefits other species associated with agro-forest open habitats (Fig. 3).

The disappearance of the undergrowth vegetation induced by the clearing results in important limitations for birds. First, species will encounter a decrease in the availability of trophic resources within the undergrowth vegetation (i.e. arthropods and fruits), a basic substrate used for feeding (Snow and Perrins, 1998). According to our own unpublished data, arthropod biomass contained in undergrowth ligneous vegetation can be very high, even higher than that recorded in the canopy layer of a mono-specific arboreal layer such as that dominating in Holm oak forests. Even the piles of accumulated fine dead branches on the ground after the clearing are a substrate apt for feeding. Second, a reduction in vegetation load may induce the loss of singing and breeding sites or other locations that may provide refuge from predators. Sites within the arboreal layers can act as an alternative for flexible species but not for selective species which focus on the use of low shrubs. Finally, changes in vegetation structure lead to changes in the microclimate of otherwise humid, dense Holm oak forests. These effects may be important for hygrophilic species especially when clearing is accompanied by tree thinning (Wren, Robin and Blackcap). In fact, microclimate has often been considered as an influential abiotic factor on bird distribution (Janzen, 1986; Lovejoy et al., 1986; Wiens, 1989), either through changes in the interactions with other species or by placing restrictions on the species physiological needs. When thinning is combined with undergrowth clearing, the loss of trophic resources and refuge substrates for more flexible undergrowth birds is enhanced and accompanied by a complete loss of forest interior microclimate. On the other hand, open conditions lead to the appearance of agro-forest habitat species, which is favoured by the fact that open meadows are often found relatively near (500–1000 m) thinned and cleared forests. This is to facilitate the use by cows of alternative pasture habitats (pers. obs.).

The structure of the remaining vegetation after clearing is another basic factor determining post-disturbance habitat use by birds. The height of the shrub layer between 1 and 2 m appears to have a critical role for undergrowth species such as the Sylvia Warblers (see also Blondel, 1981 for “garrigue” bird assemblages). The low height of the arboreal layer prevailing in Holm oak forests may help to mitigate the negative effects of sparse undergrowth for flexible species (i.e. species capable of using tree canopies to some extent) such as the Robin, the Blackbird and the Blackcap.

In thinned Holm oak forests, the reduction in tree density and associated lianas, together with the preservation of the more developed tree trunks seemed to promote the presence of trunk-foraging species. The rock cover was negatively associated with different undergrowth passerines and positively with the tits. The effect of rock cover on undergrowth birds can be interpreted as an indirect indicator of shrub cover deficiency in rocky areas (i.e. undergrowth clearing and intense thinning leave the open and the rocky outcrops visible) or as indication of dry conditions in the area. A more direct explanation may be found for tits since this group makes direct use of rocky outcrops as substrate for nest building which may be otherwise scarce in managed Holm oak forests (pers. obs.).

A site tenacity effect has been described several times in undergrowth birds (first described in Emlen (1970), and ratified by Prodon and Lebreton (1981), Prodon et al. (1987), Pons
According to this effect, birds may persist in the original territories after disturbances such as fires. The existence of tenacious birds may cushion the effects of the disturbance, since only one part of the population disappears either by death or dispersion. However, in the experimental forest clearing, the three Sylvia Warblers species most affected by the disturbance did not show tenacious behaviour after clearing of the undergrowth, probably because they found suitable habitats nearby.

To summarize the main effects of clearing and thinning of Holm oak forests on birds, it is possible to establish a gradient of response strength according to the use by species of undergrowth vegetation: (a) species that require high shrub cover and which are already scarce after partial clearing: the Subalpine Warbler, the Sardinian Warbler and the Garden Warbler; (b) species that tolerate clearing to some degree, but use, preferably, nearby non-cleared areas as breeding sites: the Blackbird and the Blackcap; (c) a group of species that remain indifferent to changes in the undergrowth, but are sensitive to decreases in undergrowth cover when applied together with tree thinning: the Wren, the Robin and the Firecrest; (d) species which tended to favour the undergrowth clearing: Nightjar; and finally, (e) tree-canopy dwelling species that enter the cleared and thinned Holm oak forests: the Turtle Dove, the Mistle Thrush, the Spotted Flycatcher, the Golden Oriole, the Serin, the Greenfinch and the Cirl Bunting.

5. Applied conclusions

The reduction of the vegetal biomass of the undergrowth is a convenient forestry practice in particular forest management circumstances. However, maintaining large extensions of forests with a low combustible load is a titanic and economically unrealizable task with obvious ecological impacts (Mesón and Montoya, 1993). Consequently, to improve biodiversity conservation it is important to ensure a certain number of patches of the different shrubs and lianas species and to apply clearing to patchy surfaces (10 ha maximum). The selection of shrubs and lianas for clearing should be applied plant by plant, so that the ligneous undergrowth is uniformly distributed, or distributed into clusters. However undisturbed small sectors no longer than 1 ha, should be reserved.

To maintain undergrowth Warbler species after clearing would require a minimum of 30–40% of shrub cover above one meter in height (preferably 1.5–2 m). Sylvia Warblers are one of the characteristic birds of Mediterranean woodlands, and therefore, they have a substantial value to conservation, in spite of not being a threatened species (Tucker and Heath, 1994). It is worth noticing, that in addition to benefiting Warbler species, preservation of the undergrowth in Holm oak forests is related to other ecological and forestry advantages such as the protection of young saplings from herbivores and the prevention of soil erosion (Mesón and Montoya, 1993).

The most intense clearings should be concentrated in the sectors with greater risk of fire, for example along forest edges near farmland areas. A complementary measurement may be to pile up part of the dry branches in small dispersed piles, of 1–2 m in diameter and at least 1 m high. These piles simulate live shrubs and when distributed sparsely throughout the clearing zone do not increase the risk of fire. In cases where there is a lack of living ligneous undergrowth, these piles may act as a refuge for arthropods, small mammals and some undergrowth birds, especially the Wren, the Robin and the Blackbird.

Finally, the management of small plots of grazed open Holm oak forest with an arboreal layer below the 400 trees/ha, might be beneficial for the protection of tree-dwelling birds, that avoid both dense Holm oak forests as well as opened spaces without trees, as long as these grazed Holm oak forests are located in convenient places (preferably neighbouring meadows) and are at least a few hectares in size. In this case, trees must grow at low density without technical rotation, until they attain large trunks and big crowns. These forests play an interesting role in the local conservation of some scarce bird species that only occur in open forests, such as Mistle Thrush, Spotted Flycatcher, Turtle Dove or Nightjar. However, these open and grazed Holm oak forests are very different ecologically to semi-natural or dense Holm oak forests, so they should not be thought of as a general management model, but as complementing the traditional forestry for firewood and wood production.

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