Cavity-nesting birds show threshold responses to stand structure in native oak forests of northwestern Tunisia

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Abstract
The detection of thresholds in forest bird response to gradients in forest alteration is a powerful approach to quantify their ecological requirements and to develop evidence-based targets for conservation. For this purpose, we analyzed the response of 31 forest bird species to a gradient in forest alteration by human activities (e.g. fire; grazing; firewood collection) in the Kroumirie region of northwestern Tunisia. We surveyed forest birds using point counts at 48 stations located throughout Feija National Park. From a data set of 12 vegetation variables, we obtained a gradient in forest alteration using a principal component analysis. Then, we modeled the probability of detection of bird species along this gradient using logistic regression. We selected the five most sensitive species as target species as indicated by the area under the receiver-operating characteristic curve (AUC). Then, we quantified thresholds in their probability of detection as a function of four habitat structure variables: density of large-diameter trees (dbh > 30 cm), canopy closure, density of snags, and downed woody material.

Nineteen of 31 species exhibited a significant response to forest alteration (PCA1), including 7 positive and 12 negative responses. Among these, the five best models (AUC > 0.8) corresponded to Levaillant’s Woodpecker (Picus vaillantii), Great Spotted Woodpecker (Dendrocopos major), Lesser Spotted Woodpecker (Dendrocops minor), Short-toed Treecreeper (Certhia brachydactyla), and Atlas Flycatcher (Ficedula speculgera). On the basis of their threshold values, we recommend to protect stands with densities of large-diameter trees of at least 650 stems ha⁻¹ and 207 stems ha⁻¹ of snags, to meet the structural requirements (90% probability of detection) of the most demanding species, respectively Levaillant’s Woodpecker and Atlas Flycatcher.

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1. Introduction
Habitat degradation is considered as one of the main threats to biodiversity worldwide (Pimm and Raven, 2000). Millennia of anthropogenic activity in native Mediterranean forests have caused a decline in critical habitat components such as large-diameter trees and dead wood (Clavero et al., 2011), along with an alteration of ecosystem processes such as natural regeneration, mainly through overgrazing (Blondel and Aronson, 1999; Plieninger, 2007) and the use of agricultural land depends on the native forests (Plieninger et al., 2011). Hence, landscapes are composed of a mosaic of native woodland, maquis and grassland (Pereira and Da Fonseca, 2003). Several studies have documented the environmental degradation in the Mediterranean basin and the resulting landscape structure (Atauri and de Lucio, 2001; Pereira and Da Fonseca, 2003; Blondel, 2006; Geri et al., 2010; Pereira et al., 2014a). Others have documented relationships between avian assemblages and habitat structure using bird occurrence and abundance data (Camprodon and Brotons, 2006; Diaz, 2006; Kati and Sekercioglu, 2006; Gil-Tena et al., 2007; Pereira et al., 2014a). A few more studies have identified potential threats to native Mediterranean oak forests and proposed management actions (Godinho and Rabaca, 2011; Robles et al., 2011; Pereira et al., 2014b).

In the Mediterranean region, Santos and Tellería (1992) and Diaz (2006) have shown that pine plantations host fewer species and a lower abundance than the primary forests they are intended to replace. Barrientos (2010) found that a habitat generalist, the Great Spotted Woodpecker (Dendrocopos major), mainly used native oak trees to nest in a landscape dominated by pine plantations. However, the breeding habitat requirements of other forest bird species in managed landscapes remain poorly documented,
especially in the southern portion of the Mediterranean basin, even though this information is critical to conservation planning.

In Tunisia, native Mediterranean oak forests persist in the mountains of the Kroumirie region, where clear felling for small scale agriculture, firewood collection, sheep and goat grazing, and anthropogenic fires threaten their persistence. In this context, it is very important to quantify the habitat requirements of species sensitive to human activities to prevent further ecological degradation and promote sustainable land use practices. To protect remnants of native vegetation and to guide their management, conservation strategies should ideally be based on empirically-derived quantitative targets (Villard and Jonsson, 2009). This approach has been applied in hemiboreal and boreal forests through the estimation of critical amounts of habitat, or habitat components, required to reach high probabilities of presence of target species (Butler et al., 2004a; Homan et al., 2004; Guénette and Villard, 2005; Roberge et al., 2008a). Thresholds have originally been sought at the landscape level (Jansson and Angelstam, 1999; Betts et al., 2007) but some researchers have also documented threshold responses to habitat components at the local scale (Büttler et al., 2004a; Roberge et al., 2008a). We must ensure that threshold ranges are consistent through time and space before using them to develop conservation targets (Betts and Villard, 2009; Müller and Büttler, 2010).

Here, we wanted (1) to determine whether forest birds of the Mediterranean basin exhibit threshold responses to local habitat structure, which might be used as targets for conservation, and (2) to fill the gap of knowledge on the quantitative habitat requirements of Mediterranean forest birds, particularly in north Africa. For this purpose, we modeled forest bird occurrence along gradients in forest alteration; we identified target species exhibiting high requirements for specific habitat parameters; and we quantified those requirements.

2. Methods

2.1. Study area

The study was conducted in Feija National Park (hereafter Feija NP), a Mediterranean ecosystem located in the Kroumirie region of northwestern of Tunisia (Fig. 1). Altitude ranges from 500 to 1200 m (Statir Peak). The climate is Mediterranean, with hot and dry summers and moist, cool winters. The annual average rainfall ranges from 800 to 1500 mm (Feija National Park weather station).

Feija NP covers 2632 ha, half (1362 ha) of which is represented by Zen oak forest. In the study area, Zen oak is found at high altitudes (800–1000 m). It is a dense forest with tall trees forming a closed canopy and, thus, an open understory. Shrubs are sparse and the herbaceous layer is practically absent. Sporadic livestock grazing contributed to prevent the development of a herbaceous stratum. Natural tree regeneration is also practically absent. Seedlings are grazed within a few years, either by livestock or by wild boars or deer. The ground is covered by a thick layer of leaf litter. Its decomposition gives a mull-humus. Cork oak forest covers 234 ha and is located at lower altitudes (600–800 m). Trees are sparsely distributed, allowing the development of a dense and varied shrub stratum dominated by Erica arborea, Arbustus unedo, Calycotome villosa, and Pistacia lentiscus. Mixed forest (zen and cork oak) covers 655 ha, shrubland covers 203 ha, and grassland covers 78 ha.

The status of National Park was attributed to El Feija forests in 1991. Since then, it is officially forbidden to log for cork, dead wood, etc. It is also prohibited to hunt or to introduce animals. However, 40 families live within the park limits and these families depend on livestock and collect firewood. Hence, there is a significant pressure on the park’s forests.

2.2. Bird surveys

We surveyed forest songbirds and woodpeckers using a modified point count method at 48 stations systematically located along wildlife trails and foot paths, at least 150 m away from the nearest road and either 450 m (in zen oak and cork oak forests) or 350 m apart (in shrubland and grassland). We chose those distances in the field using a hand-held GPS unit to reduce the risk of double-counting individuals of species, such as Levaillant’s Woodpecker (Picus vaillantii).

We conducted surveys during the 2009 breeding season, from 13 to 20 May; 25 May to 3 June and 9 to 17 June. We performed
three 15-min. counts at each station, between 0500 and 1100, when weather conditions did not interfere with bird detection (no precipitation or strong winds). Each 15 min-count was divided into three 5-min periods: 0–5 min (silent observation); 5–10 min (playback of target species’ recordings; 10–15 min (silent observation). We recorded all birds detected visually or aurally within a radius of 80 m. Species detected at <5% of our stations were excluded from statistical analyses.

2.3. Vegetation sampling

We collected vegetation data from June to July 2009 following the protocol described in Guénette and Villard (2005). We sampled three transects (80 m × 4 m) oriented to the north, southeast and southwest around each point count station. Along each transect, we measured diameter at breast height (dbh) of all trees (>30 cm dbh) and snags (>20 cm dbh) and we counted all downed trees (>10 cm at mid-length). Every 25 m, we also quantified canopy closure, canopy height, and within a 5-m radius, sapling density (>1 m high; <8 cm dbh), and visually estimated percent cover of vegetation strata (S1: 0–0.25 m, S2: 0.25–0.5 m, S3: 0.5–1 m, S4: 1–2 m, S5: 2–4 m, S6: 4–8 m) following Prodon (1981). Canopy closure was estimated by counting the squares with canopy foliage through a 5 × 5 grid (each cell: 10 cm on a side) traced on a transparent sheet of Plexiglas held overhead. We measured canopy height using a clinometer.

From these measurements, we calculated 12 variables reflecting structure or composition (percent cork oak stems) of the different habitat types in native oak forests of Feija NP (Table 1).

2.4. Statistical analyses

We used a principal component analysis (PCA) to explore gradients in vegetation structure possibly reflecting forest alteration. Transformations (logarithmic, arcsine) were applied where appropriate. We interpreted the number of significant axes and their association with particular variables using the broken-stick criterion (Peres-Neto et al., 2003) and we interpreted axes on the basis of factor loadings. The first principal component (hereafter PCA1) was interpreted as a gradient in forest alteration (see Section 3).

We also examined the relationship between the probability of detection of each target species and individual explanatory variables reflecting habitat structure using logistic regression. Model fit was assessed using the area under the curve (AUC) of a receiver-operating characteristic (ROC) plot, which ranges from 0.5 for random performance to 1.0 for perfect fit (Hosmer and Lemeshow, 2000). Following Roberge et al. (2008a,b), thresholds in species response to habitat features were defined as values of independent variables corresponding to a probability of occurrence of 0.9. This criterion is deemed conservative enough to ensure that good-quality habitat can be identified, considering that nesting habitat requirements may be higher than those associated with mere occurrence of the same species (e.g. Poulin et al., 2008). We searched for evidence of spatial autocorrelation in the residuals of logistic regression models using Moran’s I.

3. Results

3.1. Habitat structure

The PCA on habitat variables produced two significant axes, which jointly explained 67.4% of the variance in the data. The first principal component (PCA1) explained 46% of the variance and included eight significant variables (Table 1). Five variables reflecting forest habitat structure were positively related to PCA1, i.e. variables reflecting forest habitat structure were positively related to PCA1, i.e. canopy closure, density of large trees, density of downed woody

<table>
<thead>
<tr>
<th>Code</th>
<th>Variables</th>
<th>PCA 1</th>
<th>PCA 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Var1</td>
<td>Density of trees &gt;30 cm dbh (stems ha⁻¹)</td>
<td>0.678</td>
<td>0.186</td>
</tr>
<tr>
<td>Var2</td>
<td>Sapling density (stems ha⁻¹)</td>
<td>-0.391</td>
<td>0.358</td>
</tr>
<tr>
<td>Var3</td>
<td>Density of snags (stems ha⁻¹)</td>
<td>0.623</td>
<td>-0.066</td>
</tr>
<tr>
<td>Var4</td>
<td>Density of downed wood (stems ha⁻¹)</td>
<td>0.823</td>
<td>-0.038</td>
</tr>
<tr>
<td>Var5</td>
<td>Canopy height (m)</td>
<td>0.703</td>
<td>0.093</td>
</tr>
<tr>
<td>Var6</td>
<td>Percent canopy closure (%)</td>
<td>0.910</td>
<td>0.008</td>
</tr>
<tr>
<td>Var7</td>
<td>Ratio of cork oak (%)</td>
<td>-0.674</td>
<td>0.387</td>
</tr>
<tr>
<td>Var8</td>
<td>Percent cover of vegetation layer (0.25–0.5 m)</td>
<td>-0.890</td>
<td>0.002</td>
</tr>
<tr>
<td>Var9</td>
<td>Percent cover of vegetation layer (0.5–1 m)</td>
<td>-0.657</td>
<td>0.300</td>
</tr>
<tr>
<td>Var10</td>
<td>Percent cover of vegetation layer (1–2 m)</td>
<td>-0.029</td>
<td>0.891</td>
</tr>
<tr>
<td>Var11</td>
<td>Percent cover of vegetation layer (2–4 m)</td>
<td>0.133</td>
<td>0.884</td>
</tr>
<tr>
<td>Var12</td>
<td>Percent cover of vegetation layer (4–6 m)</td>
<td>0.096</td>
<td>0.836</td>
</tr>
<tr>
<td>Strata</td>
<td>Eigenvalue</td>
<td>5.981</td>
<td>2.786</td>
</tr>
<tr>
<td>Variance explained (%)</td>
<td>46.009</td>
<td>21.434</td>
<td></td>
</tr>
<tr>
<td>Cumulative variance explained (%)</td>
<td>46.009</td>
<td>67.443</td>
<td></td>
</tr>
</tbody>
</table>

The bold characters signifies the highest correlation with the axis in terms of absolute value.

* dbh = Diameter at breast height.

Fig. 2. Distribution of the 48 point count stations in a principal component analysis (PCA) biplot based on local vegetation variables. Symbols correspond to the dominant habitat types present. The ellipse corresponds to the least degraded stations, characterized by a high density of large trees, snags, and downed woody material.
material, canopy height, and density of snags. The three other variables (percent cover of vegetation layer 0.25–0.5 m, ratio of cork oak and percent cover of vegetation layer 0.5–1 m) were negatively associated to PCA1. This principal component separated stations as a function of stand structure, with those characterized by a high density of large trees and snags and downed woody material located to the right of the PCA biplot (Fig. 2). To the left, stations were characterized by an open canopy with a dense bushy

### Parameters of logistic regression models relating the probability of detection of the five most sensitive species to critical habitat parameters.

Table 2

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Freq</th>
<th>Resp</th>
<th>Univariate logistic regression model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$b_1^*$</td>
</tr>
<tr>
<td>Short-toed Treecreeper</td>
<td>Certhia brachydactyla</td>
<td>0.67</td>
<td>–</td>
<td>2.44 ± 0.72</td>
</tr>
<tr>
<td>Atlas Flycatcher</td>
<td>Ficedula speculigeria</td>
<td>0.60</td>
<td>–</td>
<td>3.31 ± 1</td>
</tr>
<tr>
<td>Levillard’s Woodpecker</td>
<td>Picus vaillanti</td>
<td>0.62</td>
<td>–</td>
<td>2.72 ± 0.71</td>
</tr>
<tr>
<td>Great Spotted Woodpecker</td>
<td>Dendrocopos major</td>
<td>0.65</td>
<td>–</td>
<td>2.54 ± 0.71</td>
</tr>
<tr>
<td>Lesser Spotted Woodpecker</td>
<td>Dendrocopos minor</td>
<td>0.49</td>
<td>–</td>
<td>1.71 ± 0.52</td>
</tr>
<tr>
<td>Eurasian Jay</td>
<td>Garrulus glandarius</td>
<td>0.42</td>
<td>–</td>
<td>2.35 ± 0.65</td>
</tr>
<tr>
<td>Coal Tit</td>
<td>Periparus ater</td>
<td>0.54</td>
<td>–</td>
<td>1.56 ± 0.4</td>
</tr>
<tr>
<td>Great Tit</td>
<td>Parus major</td>
<td>0.71</td>
<td>–</td>
<td>2.47 ± 0.7</td>
</tr>
<tr>
<td>Common Wood-pigeon</td>
<td>Columbia palumbus</td>
<td>0.21</td>
<td>–</td>
<td>1.75 ± 0.6</td>
</tr>
<tr>
<td>Eurasian Chaffinch</td>
<td>Fringilla coelebs</td>
<td>0.71</td>
<td>–</td>
<td>0.40 ± 0.31</td>
</tr>
<tr>
<td>Firecrest</td>
<td>Regulus ignicapillus</td>
<td>0.44</td>
<td>–</td>
<td>0.87 ± 0.2</td>
</tr>
<tr>
<td>Bonelli’s Warbler</td>
<td>Phylloscopus bonelli</td>
<td>0.29</td>
<td>–</td>
<td>0.19 ± 0.31</td>
</tr>
<tr>
<td>Common Stonechat</td>
<td>Saxicola torquatus</td>
<td>0.21</td>
<td>+</td>
<td>–4.94 ± 2.1</td>
</tr>
<tr>
<td>Sardinian Warbler</td>
<td>Sylvia melanocephala</td>
<td>0.40</td>
<td>+</td>
<td>–2.33 ± 0.65</td>
</tr>
<tr>
<td>Blackcap</td>
<td>Sylvia atricapilla</td>
<td>0.29</td>
<td>+</td>
<td>–0.90 ± 0.32</td>
</tr>
<tr>
<td>Dartford Warbler</td>
<td>Sylvia undata</td>
<td>0.20</td>
<td>+</td>
<td>–2.45 ± 1</td>
</tr>
<tr>
<td>Cirl Bunting</td>
<td>Emberiza cirrus</td>
<td>0.20</td>
<td>+</td>
<td>–0.75 ± 0.32</td>
</tr>
<tr>
<td>Wren</td>
<td>Troglodytes troglodytes</td>
<td>0.50</td>
<td>+</td>
<td>–0.57 ± 0.21</td>
</tr>
<tr>
<td>European Robin</td>
<td>Estricasus rubecula</td>
<td>0.77</td>
<td>+</td>
<td>–0.10 ± 0.3</td>
</tr>
</tbody>
</table>

### Parameters of logistic regression models relating the probability of detection of the five most sensitive species to critical habitat parameters.

Table 3

<table>
<thead>
<tr>
<th>Density of trees ≥ 30 cm dbh (stems ha$^{-1}$)</th>
<th>$b_1^*$</th>
<th>$b_0^+$</th>
<th>AUC $p$-value</th>
<th>$X_{0.9}^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-toed Treecreeper</td>
<td>0.041 ± 0.015</td>
<td>–0.52 ± 0.2</td>
<td>0.854 $^{**}$</td>
<td>67</td>
</tr>
<tr>
<td>Levillard’s Woodpecker</td>
<td>0.015 ± 0.006</td>
<td>–0.613 ± 0.3</td>
<td>0.766 $^{*}$</td>
<td>188</td>
</tr>
<tr>
<td>Great Spotted Woodpecker</td>
<td>0.048 ± 0.01</td>
<td>–0.772 ± 0.036</td>
<td>0.844 $^{**}$</td>
<td>63</td>
</tr>
<tr>
<td>Lesser Spotted Woodpecker</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Atlas Flycatcher</td>
<td>0.017 ± 0.006</td>
<td>–1.13 ± 0.35</td>
<td>0.742 $^{*}$</td>
<td>207</td>
</tr>
</tbody>
</table>

### Density of downed wood (stems ha$^{-1}$)

<table>
<thead>
<tr>
<th>Density of downed wood (stems ha$^{-1}$)</th>
<th>$b_1^*$</th>
<th>$b_0^+$</th>
<th>AUC $p$-value</th>
<th>$X_{0.9}^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-toed Treecreeper</td>
<td>0.016 ± 0.007</td>
<td>–0.13 ± 0.3</td>
<td>0.855 $^{*}$</td>
<td>198</td>
</tr>
<tr>
<td>Levillard’s Woodpecker</td>
<td>0.022 ± 0.008</td>
<td>–1.158 ± 0.36</td>
<td>0.85 $^{*}$</td>
<td>154</td>
</tr>
<tr>
<td>Great Spotted Woodpecker</td>
<td>0.011 ± 0.005</td>
<td>–0.054 ± 0.29</td>
<td>0.791 $^{*}$</td>
<td>213</td>
</tr>
<tr>
<td>Lesser Spotted Woodpecker</td>
<td>0.006 ± 0.003</td>
<td>–1.51 ± 0.34</td>
<td>0.729 $^{*}$</td>
<td>180</td>
</tr>
<tr>
<td>Atlas Flycatcher</td>
<td>0.008 ± 0.003</td>
<td>–1.092 ± 0.3</td>
<td>0.788 $^{*}$</td>
<td>122</td>
</tr>
</tbody>
</table>

### Density of trees ≥ 30 cm dbh (stems ha$^{-1}$)

<table>
<thead>
<tr>
<th>Density of trees ≥ 30 cm dbh (stems ha$^{-1}$)</th>
<th>$b_1^*$</th>
<th>$b_0^+$</th>
<th>AUC $p$-value</th>
<th>$X_{0.9}^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-toed Treecreeper</td>
<td>0.01 ± 0.003</td>
<td>–1.973 ± 0.6</td>
<td>0.902 $^{**}$</td>
<td>426</td>
</tr>
<tr>
<td>Levillard’s Woodpecker</td>
<td>0.006 ± 0.002</td>
<td>–2.027 ± 0.6</td>
<td>0.788 $^{**}$</td>
<td>653</td>
</tr>
<tr>
<td>Great Spotted Woodpecker</td>
<td>0.008 ± 0.002</td>
<td>–1.647 ± 0.4</td>
<td>0.861 $^{**}$</td>
<td>490</td>
</tr>
<tr>
<td>Lesser Spotted Woodpecker</td>
<td>0.004 ± 0.002</td>
<td>–2.265 ± 0.64</td>
<td>0.712 $^{**}$</td>
<td>480</td>
</tr>
<tr>
<td>Atlas Flycatcher</td>
<td>0.007 ± 0.002</td>
<td>–2.961 ± 0.65</td>
<td>0.833 $^{**}$</td>
<td>516</td>
</tr>
</tbody>
</table>

### Canopy closure (%)

<table>
<thead>
<tr>
<th>Canopy closure (%)</th>
<th>$b_1^*$</th>
<th>$b_0^+$</th>
<th>AUC $p$-value</th>
<th>$X_{0.9}^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short-toed Treecreeper</td>
<td>0.06 ± 0.018</td>
<td>–1.355 ± 0.6</td>
<td>0.877 $^{**}$</td>
<td>53.72</td>
</tr>
<tr>
<td>Levillard’s Woodpecker</td>
<td>0.065 ± 0.017</td>
<td>–2.369 ± 0.76</td>
<td>0.873 $^{**}$</td>
<td>70.71</td>
</tr>
<tr>
<td>Great Spotted Woodpecker</td>
<td>0.061 ± 0.017</td>
<td>–1.361 ± 0.6</td>
<td>0.863 $^{**}$</td>
<td>58.72</td>
</tr>
<tr>
<td>Lesser Spotted Woodpecker</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Atlas Flycatcher</td>
<td>0.05 ± 0.015</td>
<td>–2.529 ± 0.79</td>
<td>0.793 $^{**}$</td>
<td>78.43</td>
</tr>
</tbody>
</table>

ns (Non-significant).

$^{*}$ P < 0.05.

$^{**}$ P < 0.01.

$^{***}$ P < 0.001.

$^a$ Parameter estimate.

$^b$ Constant.

$^c$ Area under the ROC curve. P-value refers to the null hypothesis of AUC = 0.5.

$^d$ Value of the predictor variable corresponding to a probability of detection of 0.9.
(0.25–1 m) stratum. Hence, PCA1 shows a gradient from degraded sites (maquis shrubland) to the least impacted ones (high-density oak forest with downed wood and snags). Thus, we interpret this axis as a gradient in forest alteration.

PCA2 explained 21.4% of variance and was positively associated with vegetation cover of three strata spanning 1–6 m in height. Stations related to PCA 2 were distinguished by the complexity of vegetation structure.

3.2. Gradient in forest alteration and bird species response

We detected a total of 42 bird species, 31 of which occurred at more than 5% of the stations. The three most frequent species were African Blue Tit (*Cyanistes teneriffae*) (96%), European Robin (*Erithacus rubecula*) (77%) and Eurasian Blackbird (*Turdus merula*) (72%).

Of the 31 species included in the analyses, the probability of detection of 19 was significantly ($p < 0.01$) related to PCA1 (Table 2). Of those 19 species, 12 responded negatively to forest alteration and 7 responded positively (Table 2).

Five species responded strongly to forest alteration (PCA1), according to the performance of the corresponding models (AUC > 0.80; Table 2): three primary cavity nesters (Levaillant’s Woodpecker, Great Spotted Woodpecker, Lesser Spotted Woodpecker) and two secondary cavity nesters or natural cavity users (Atlas Flycatcher and Short-toed Treecreeper). Hereafter, we will focus on these five target species to quantify specific forest habitat requirements. Of these, the Lesser Spotted Woodpecker seemed to be the most sensitive to forest alteration, according to its threshold value along the gradient in forest alteration (PCA1) (Table 2). The other target species, in decreasing order of sensitivity to forest alteration, were Atlas Flycatcher, Levaillant’s Woodpecker, Great Spotted Woodpecker, and Short-toed Treecreeper.

Species benefiting from forest conversion to shrubland were European Robin, Wren, Cirl Bunting, Dartford Warbler, Blackcap, Sardinian Warbler and Common Stonechat. The latter two species had the best models, according to the AUC value (AUC > 0.8). However, given Common Stonechat’s low frequency of occurrence (0.20), this result must be interpreted with caution (see Guénette and Villard, 2004).

3.3. Evidence for thresholds in habitat requirements

All target species responded strongly (AUC > 0.75) to the density of large-diameter trees (dbh > 30 cm). Threshold values ($p = 0.9$) ranged from 426 stems ha$^{-1}$ for Short-toed Treecreeper to 653 stems ha$^{-1}$ for Levaillant’s Woodpecker. Similarly, models based on the density of downed wood performed well for all target species. Threshold values ranged from 122 to 213 stems ha$^{-1}$ for Atlas Flycatcher and Great Spotted Woodpecker, respectively. Logistic regression models based on the snag density and canopy

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**Fig. 3.** Logistic regression models showing the response of target bird species to parameters of forest stand structure. Those species responded most strongly (AUC > 0.83) to the habitat structure variables considered. Broken lines indicate thresholds in stand structure corresponding to a 90% probability of detection of the corresponding species.
closure also performed well (AUC > 0.74) for all species except Les-
sser Spotted Woodpecker. A high threshold value for snags was
recorded for the Atlas Flycatcher (207 stems ha⁻¹), compared to
67 stems ha⁻¹ for Short-toed Treecreeper (Table 3).

4. Discussion

To our knowledge, this is one of the first studies investigating
thresholds in the response of cavity-nesting birds to forest alter-
ation in the African portion of the Mediterranean region. Primary
cavity-nesting birds have been used as target species to develop
evidence-based conservation strategies in many forest regions of
the world (Gunn and Hagan Iii, 2000; Angelstam et al., 2003;
Bütler et al., 2004a,b; Roberge et al., 2008a,b; Edman et al.,
2011). Several species of woodpeckers are known to be es-
specially sensitive to forest stand structure (Roberge et al., 2008a;
Robles et al., 2011) and they have been shown to be good surrogates for
passerine bird species (Mikusinski et al., 2001). In this study, we
found five species that were particularly sensitive to forest degra-
dation by human activities, in particular firewood collection. Three
species of woodpeckers, a secondary cavity nester (Atlas Fly-
catcher), and a species mainly nesting in natural crevices (Short-
toed Treecreeper; Moez Touihri, unpublished data).

Among the three species of woodpeckers, only the Lesser Spot-
ted Woodpecker did not respond significantly to the density of
snags and to canopy closure. This seems surprising for a forest spe-
cialist, but Roberge et al. (2008a) also found that the relationship
between its occurrence and the density of dead wood was not sig-
nificant in some portions of its range. This species mainly forages
on dead branches on live trees in Europe (Roberge et al., 2008a
and references therein). This may apply to our study area as well.
For the other two woodpecker species, all threshold values were
highly significant. However, Levaiellant’s Woodpecker seemed to
be more demanding than the Great Spotted Woodpecker, except
for the density of downed woody material (≥ 10 cm diameter),
where the former had lower requirements. This is expected given
the foraging behavior of Levaiellant’s Woodpecker, which captures
ants and other insects directly on the ground (Whitaker, 1905;
Meinertzhagen, 1940).

Generally, secondary cavity-nesting birds are expected to be
influenced by forest habitat alteration. In fact, Robles et al.
(2011) have shown that some traditional human practices in old
oak forests such firewood collection and selective cutting can influ-
ence cavity abundance and occupancy, hence reproductive per-
fomance of secondary cavity nesters such as the Atlas Flycatcher,
a species endemic to North Africa (Isernmann et al., 2005), which
was the most demanding of our target species in terms of snag
density and canopy closure.

On the basis of their threshold values (Table 3, Fig. 3), we rec-
ommend to protect stands with densities of large-diameter trees
of at least 650 stems ha⁻¹, and 207 stems ha⁻¹ of snags, to meet
the structural requirements of the most demanding species,
respectively Levaiellant’s Woodpecker and Atlas Flycatcher. Those
thresholds correspond to probabilities of occurrence of 0.9, hence
are relatively conservative. These proposed targets should be seen
as working hypotheses for management rather than as strict guide-
lines. Indeed, the analyses present some limitations. First, data on
presence–absence during the breeding season may underestimate
habitat requirements for successful nesting (e.g. Poulain et al.,
2008). However, collecting fitness data on several species at the
landscape scale is very time-consuming. Hence, models based on
probability of detection are likely to remain a major source of
information for defining conservation targets until more efficient
methods to estimate fitness are developed.

5. Conclusion

Our findings suggest that cavity-nesting birds and the highly
specialized treecreeper are strongly linked to structures associated
with old forests. Thus, the critical resources used by these species
should be protected or restored wherever possible. Those critical
habitat components are snags, large-diameter trees, downed
woody material, as well as canopy closure. In the absence of
research on the same species in other locations, the threshold val-
ues provided here should be used with caution to develop evi-
dence-based conservation targets for this and other oak forests
of Tunisia such as Bni Mtit forests (36°43′56″N; 8°41′58″E), in
the northwestern part of the country.

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