# Bird Community Responses to Vegetation Heterogeneity Following Non-Direct Regeneration of Mediterranean Forests after Fire

Authors: Zozaya, Elena L., Brotons, Lluís, and Vallecillo, Sara

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# Bird community responses to vegetation heterogeneity following non-direct regeneration of Mediterranean forests after fire

**Elena L. Zozaya[1,*], Lluís Brotons[1] & Sara Vallecillo[1]**

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Mediterranean forests are highly resilient to fires, showing a rapid recovery after disturbance. However, in some cases direct tree regeneration fails leading to radical changes in landscape composition. In this study, we evaluated the impact of landscape changes on the conservation value of bird species using the new landscape mosaic arising from non-direct regeneration after a fire. We used data from a large fire that occurred in central Catalonia (NE Spain) in 1998. The fire affected about 26,000 ha of a land mosaic mainly covered by Black Pine *Pinus nigra* forests and farmland dominated by cereal crops. We used line transects to estimate bird abundance and gathered information on dominant vegetation covers and landscape variables. Redundancy analysis (RDA) and generalized linear models were used to explore how the measured environmental variables explain bird species abundance and to analyze how post-fire heterogeneity in vegetation affected the conservation value of the bird community. Factors describing the main patterns in the post-fire landscape explained up to 31.2% of the total variability in bird community composition and described three main groups of bird species sharing similar ecological requirements. Additionally, 71% of the studied species significantly responded to one of the first three vegetation gradients distinguished in the study area. Finally, the conservation value of the bird community significantly decreased in areas dominated by *Q. humilis* resprouters and significantly increased in shrubland areas. Overall, our results suggest that large fires affecting non-direct regenerating forest types lead to a new and radically different mosaic landscape offering new opportunities to species with unfavourable European conservation status.

Key words: conservation value, large fires, open-habitat bird species, *Pinus nigra*, regeneration patterns, shrubland

[1]Forest Technology Centre of Catalonia, Biodiversity Department-Landscape Ecology Group, Ctra. de St. Llorenç de Morunys a Port del Comte km 2, 25280 Solsona, Spain;
*corresponding author (elzozaya@gmail.com)

Fires are the most important natural disturbance in Mediterranean regions, and exert a decisive role in the dynamics and structure of plant and animal communities (di Castri & Mooney 1973, Picket & White 1985, Whelan 1995). The effect of fires on biological diversity is highly variable and depends, among other factors, on characteristics such as extent and intensity of the fire (Sousa 1984), the initial state of the ecosystem (Christensen 1993, Foster *et al.* 1998) and the biotic and abiotic environment (Foster *et al.* 1998).

Due to their ability to fly, birds can often avoid the direct effects of flames through moving into adjacent habitats not affected by the passage of fire (Lawrence 1966). Nevertheless, the drastic modification of habitat has important consequences on the re-colonisation of the burnt area. Due to their strong site tenacity, philopatry, habitat tolerance, and to the persistence of standing dead trees, some forest bird species can return to burnt territories the first breeding season after fire, but they progressively leave their breeding territories and do not reappear until the vegetation attains a woody appearance (Prodon *et al.* 1987, Pons & Prodon 1996). Apart from these cases, the post-fire succession of bird communities is closely linked with vegetation recovery, first starting with open-habitat species, then shrubland species and finally forest species (Prodon *et al.* 1984, Jacquet & Prodon 2009). Overall, forest bird species are the most negatively affected by fire (Ukmar *et al.* 2007) while open-habitat species seem to have greatly benefited from it (Pons & Bas 2005). In fact, recent literature has highlighted the role of burnt areas in the Mediterranean region in the maintenance of open-habitat bird species populations (Brotons *et al.* 2008, Vallecillo *et al.* 2009). This is especially relevant since these species are among the most threatened species in Europe (Birdlife International 2004). Pons & Bas (2005) showed that 17 out of 22 open-habitat bird species using recently burnt areas in Iberia and southern France had an unfavourable conservation status in Europe. Thus, beyond the direct effect of fire, the structure of bird communities after fire seems to be highly dependent on the effect of fire on habitat composition, increasing species diversity with habitat heterogeneity and time since disturbance (Herrando *et al.* 2002, Herrando *et al.* 2003, Ukmar *et al.* 2007, Vallecillo *et al.* 2008).

In this sense, it is widely accepted that Mediterranean vegetation is highly resilient to the effects of fire; this means that the same pre-disturbance community is restored only a few decades after the disturbance (Hanes 1971, Lloret 1998). Nevertheless, recent studies showed that heterogeneous landscapes can arise in relatively homogeneous forest areas after a large forest fire when dominant pre-fire tree forest species fail in direct regeneration (e.g. large forest fires of Black Pine *Pinus nigra* in Catalonia, northeastern Spain, Retana *et al.* 2002; Rodrigo *et al.* 2004). Under such circumstances, the change in forest cover results in post-fire environmental conditions completely different from those of unburnt *Pinus nigra* forests. Hereafter, we refer to this process as non-direct regeneration. In addition, the low colonisation ability of *Pinus nigra* (Ordoñez *et al.* 2004) allows differences in forest structure to prevail for decades, favouring the persistence of newly appearing species. Since bird communities respond to changes in vegetation composition and structure caused by fire (Prodon & Lebreton 1981), these landscape changes, caused by a non-direct regeneration, are expected to enhance bird diversity and favour the persistence of colonisers.

To date, most studies on the effects of fire on birds in the Mediterranean Basin have been carried out in study areas highly resilient to fire where local communities return to their former state after fire disturbance (e.g. Prodon & Lebreton 1981, Prodon *et al.* 1984, Pons & Prodon 1996, Herrando *et al.* 2002, Jacquet & Prodon 2009). However, to the best of our knowledge, there is no study analyzing the post-fire bird community under a non-direct regeneration scenario. In this work, we examined how spatial differences in bird community structure appearing after fire track patterns of vegetation recovery. In the case of the diverse landscape mosaic arising in response to the lack of direct regeneration of pre-fire dominating pines, we expected to find a mosaic of bird communities matching the heterogeneity in vegetation. Finally, we analyzed to what extent post-fire heterogeneity in vegetation recovery affects the conservation value of the bird community.

## METHODS

### Study area

The study area is located in the Solsonès county (41°59'–41°44' N, 1°21'–1°39' E, Lleida, northeastern Spain), in an area characterized by a marked altitudinal gradient, decreasing towards the south, with altitudes that range from 450 to 950 m above sea level. In July 1998, several fires burnt around 26,000 ha (Fig. 1), which was mostly affected by crown fire (*sensu* Turner *et al.* 1994); all trees were killed and canopy needles were completely burnt.

According to the data collected in 1993 for the Ecological Forest Inventory of Catalonia (IEFC) 67% of the total burnt area affected forested lands, with the remaining land dominated by cereal crop-fields (Gracia *et al.* 2000). Hence, the burnt area comprised a continuous forest mass on sloping areas with agricultural patches located in flat terrains. The main forest species affected were Black Pine *Pinus nigra* (74%) together with Aleppo Pine *Pinus halepensis* (11%), with Holm Oak *Quercus ilex* and the deciduous species Lusitanian Oak *Quercus faginea*. The understory was mainly covered by Downy Oak *Quercus humilis*. *Pinus nigra* is a non-resprouter species with a regeneration strategy based on germination. As its seeds are dispersed in spring (Skordilis & Thanos 1997, Alvarez *et al.* 2007), summer fires prevent the regeneration and recovery of stands of this species, leading to regeneration of a different type of forest dominated by resprouting species such as oaks (Habrouk *et al.* 1999, Rodrigo *et al.* 2004). In the study area, the forest landscape changed to a mosaic of different habitats dominated by different *Quercus* species, shrubland and open grasslands with

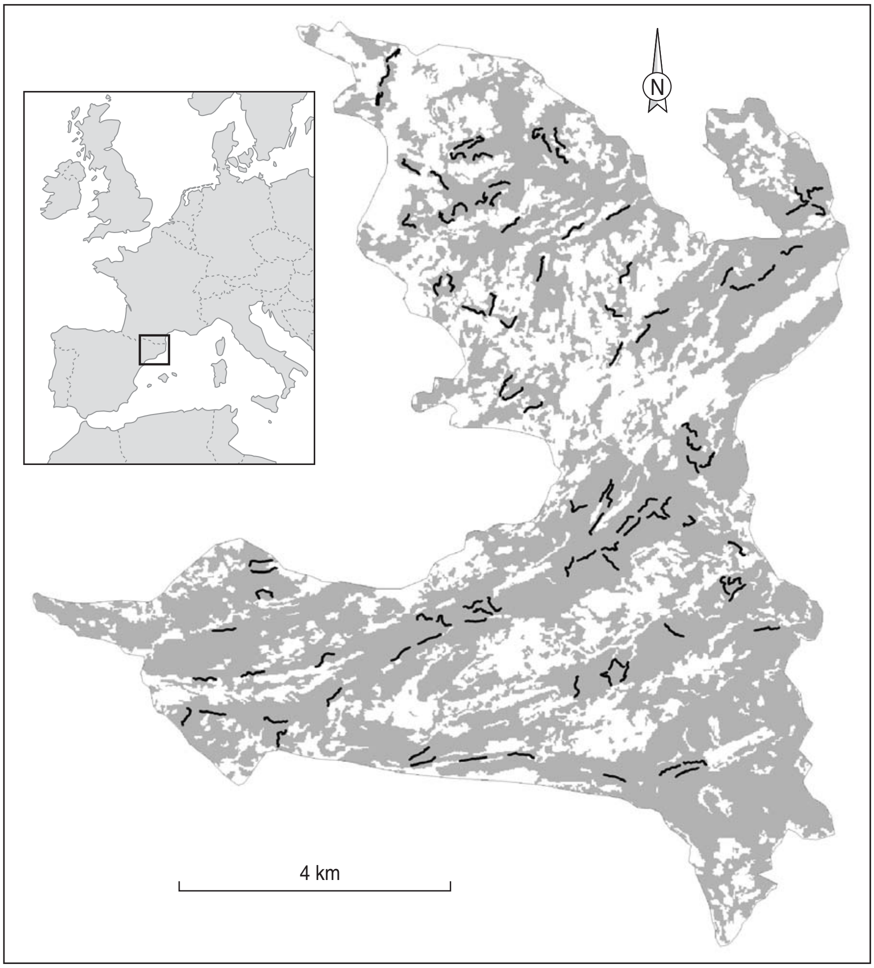


**Figure 1.** Map of the large forest fire in the Solsonès county in 1998. Fire perimeter (grey line) and transect locations (black lines) are shown. The area shown represents burnt habitats, with grey representing burnt forests and white accounting for agricultural areas (mainly cereals).

some remains of unburnt *Pinus nigra* (Retana *et al.* 2002) thereby increasing habitat heterogeneity.

**Field surveys**

We used line transects to estimate bird presence and abundance (Bibby *et al.* 2000). Each transect took 20 minutes to walk and covered about 700 m in length (range 602–820 m). Birds were counted, when heard or seen, within 100 m belts on both sides of the track. Censuses were conducted in 2005, 7 years after the fire. Each transect was surveyed twice, with one visit in the early breeding season (19 April – 24 May) and one in the middle of the breeding season (24 May – 24 June), allowing approximately 1 month between visits to the same transect. The higher of the two counts per species was used as the dependent variable for further analysis. Raptors, aerial feeders (swallows, swifts and bee-eaters) and crepuscular species were excluded from the analysis because this method is not appropriate to assess their abundance (Bibby *et al.* 2000).

Transects were distributed within the burnt area using random stratified sampling. We randomly located 25 points within the fire perimeter. At each of these points (approximately 2 km radius), 4 survey transects were defined (Fig. 1). We used four criteria to select the transect location around each point: 1) Transects were located in burnt natural habitat, 2) Transects were easily accessible from walking trails, 3) Transects represented the main burnt habitat types occurring near the random point, 4) The minimum distance between transects was 200 m. All bird surveys were performed by the same observer, and were always conducted in good weather conditions (i.e. without rainfall or strong wind). All transects were conducted within 3 hours from sunrise.

Habitat characteristics were recorded along each transect using a modification of the cover estimation method proposed by Prodon & Lebreton (1981), which involves a visual estimation of the relative percentage cover of each variable within a defined area, in this case the transect. The following vegetation layers were measured: bare ground, rock cover, herbaceous vegetation (0–0.25 m), shrubby vegetation (0.25–1 m) and an overall assessment of the cover of three regenerating tree species (*P. halepensis, Q. ilex* and *Q. humilis*). These covers were taken to be representative of the whole length of transects, including a 100 m belt on both sides. They were recorded in both visits and mean values were used as explanatory variables for further analysis. Recent work carried out in the same study area has shown that our field vegetation cover estimates reliably represented major components of variability in vegetation cover along the transects calculated using Satellite Landsat data (Normalized Difference Vegetation Index, NDVI, Pettorelli *et al.* 2005) (Menz *et al.* 2009).

Finally, considering the importance of landscape variables in explaining ecological processes such as regeneration patterns (Turner *et al.* 1994) and fauna distribution (Izhaki & Adar 1997, Vallecillo *et al.* 2008, Menz *et al.* 2009), the following variables were estimated within 250 m belts of the transects: (1) Slope was calculated using a Digital Elevation Model (DEM) generated from 1:50,000 topography maps, (2) Aspect was measured as the proportion of south and north-facing pixels, (3) The relative abundance of surrounding agricultural fields, unburned patches, standing and laying dead burnt trunks and streams within the 100 m belt at each side of the transect were estimated in the field (categorical, 1–3 with increasing abundance).

**Data analyses**

The relationship between bird species and environmental variables was analyzed. Due to the relatively large number of environmental variables (initially 14) we firstly performed a Principal Components Analysis (PCA, Statistica v.6; StatSoft 2001) to reduce the number of variables and reduce colinearity between variables. We used a PCA with a varimax normalized rotation. This procedure maximizes the correspondence between the factors and the original variables. We retained the minimum number of components where all original variables were represented and used them for further analyses.

We performed a Redundancy Analysis (RDA; ter Braak 1986) to relate the bird community with the main factors described in the PCA. This method assumes that species are responding linearly to the ordination axis. Species linear response was tested using a Detrended Correspondence Analysis (DCA). Species abundance was Log-transformed in order to prevent a skewed distribution and a Monte-Carlo permutation test was performed to determine the significance of the first ordination axis and that of all canonical axes together. This RDA analysis was run within the CANOCO program version 3.2 (ter Braak 1988). Additionally, species-specific analyses were performed using generalized linear models (GLM) and generalized linear mixed models (GLMM) to describe ecological requirements for each species (Dobson 1990), (R Development Core Team 2008). We used the abundance of each species found in each transect as the response variable and the main vegetation gradients described by the PCA as fixed factors for this analysis. We used a Poisson distribution and a log-link function for the dependent variable. In the cases where there was a significant site effect on species distribution we performed a GLMM considering site as a random factor in the analysis. However, we performed a GLM when site did not have an effect on the species distribution. For either the RDA, GLM or GLMM analyses explained above, we only considered those species recorded in more than 5% of the transects (see Appendix 1).

Finally, we analyzed to which degree post-fire heterogeneity in vegetation recovery affects the conservation value of the bird community. With this purpose, we used a Conservation Index that takes into account the conservation status and abundance of the species recorded in each transect (Pons *et al.* 2003). The status was based on the classification of Birdlife International (2004) in categories of "Species of European Conservation Concern", hereafter SPEC. A SPEC value was assigned to each species in geometric progression of increasing conservation concern (SPEC value$_i$: Non-SPEC =1, SPEC-3 =2, SPEC-2 =4, SPEC-1 =8). In the present study, species belonging to all categories except SPEC-1 were recorded (see Appendix 1). Abundance was log-transformed to balance its contribution to the global index.

$$Conservation\ Index = \sum_{i=1}^{k} \left[\log(A_i + 1) \times SPECvalue_i\right],$$

where $k$ is the species richness and $A_i$ the abundance of species $i$ recorded in each transect and relative to an area of 1 ha.

The influence of main vegetation gradients on the Conservation Index relative to each transect was then assessed by a GLM. We used the Conservation Index on each transect as the response variable and the main vegetation gradients described by the PCA as fixed factors. The normal distribution of the dependent variable was checked using the plot package within R software.

## RESULTS

### Post-fire regeneration patterns

The principal component analysis summarised environmental variability in post-fire regeneration patterns in seven factors explaining 80% of the original variability in the regeneration patterns (Table 1). The first factor (*Quercus humilis regeneration*) explained about 34% of the variability and represented a gradient of decreasing regeneration of *Q. humilis*, dominating northern slopes, to areas with virtually no regeneration of this deciduous oak species and increasing surface of bare soil in southern dominated slopes. The second factor (*Farmland*) separated zones characterized by the presence of farmland, extensive cereal fields and unburnt patches in flatter areas, from those homogenously burnt in more abrupt topography. The third factor (*Shrubland*) represented a gradient of decreasing shrub cover with increasing low, herbaceous vegetation. The fourth factor (*Pine regeneration*) was related to the pine resprouters of the species *P. halepensis*. The fifth factor (*Standing trunks*) was related mainly to the amount of standing and laying dead burnt trunks generated in post-fire salvage logging and management activities undergone during the first two years after fire. The sixth factor (*Stream*) was related to the presence of riparian areas in which vegetation had recovered rapidly but only locally along the stream sides. Finally the last factor (*Quercus ilex regeneration*) identified locations with strong re-sprouting of *Q. ilex*.

### Bird community

Overall, we found that factors describing the main patterns in the post-fire landscape explained up to 31.2% of the total variability in bird community composition. A plot of the first two axes of the RDA is shown in Figure 2. The first axis reflected a gradient of vegetation structure from shrublands to deciduous *Q. humilis* resprouters. The second axis separated farmland from the remainder of the land use types. The plot described three main species groups that share similar ecological requirements. The first group was characterised by species using areas where resprouters of *Quercus* species dominated the post-fire regeneration,

**Table 1.** Principal Components Analysis performed on habitat characteristics and landscape variables. Main contributing variables are given in bold. Seven factors loading for each individual variable were obtained using a varimax normalized rotation. The percentage of accumulated variation is 80.2%.

| | F1 *Quercus humilis* regeneration | F2 Farmland | F3 Shrubland | F4 Pine regeneration | F5 Standing trunks | F6 Stream | F7 *Quercus ilex* regeneration |
|---|---|---|---|---|---|---|---|
| Habitat characteristics | | | | | | | |
| Rock cover | –0.64 | –0.14 | 0.37 | –0.11 | 0.13 | 0.14 | 0.43 |
| Bare ground | **–0.65** | –0.27 | 0.50 | –0.04 | –0.01 | –0.15 | 0.06 |
| Herbaceous vegetation | –0.06 | –0.07 | **–0.84** | –0.05 | –0.15 | 0.22 | –0.04 |
| Shrub vegetation | –0.33 | –0.08 | **0.75** | 0.01 | 0.07 | 0.16 | 0.15 |
| *Quercus ilex* resprouts | –0.24 | 0.14 | 0.13 | 0.05 | 0.01 | 0.01 | **0.87** |
| *Pinus halepensis* resprouts | –0.08 | –0.06 | 0.03 | **0.94** | –0.03 | –0.11 | 0.04 |
| *Quercus humilis* resprouts | **0.82** | 0.17 | –0.22 | –0.15 | 0.09 | –0.21 | –0.11 |
| Landscape variables | | | | | | | |
| Slope | –0.35 | **–0.57** | 0.44 | 0.13 | 0.02 | 0.27 | –0.13 |
| North orientation | **0.84** | –0.17 | –0.12 | 0.04 | –0.08 | –0.02 | 0.03 |
| South orientation | **–0.79** | –0.06 | 0.23 | –0.14 | 0.05 | –0.07 | –0.02 |
| Agricultural fields | –0.01 | **0.78** | –0.14 | –0.12 | 0.04 | –0.14 | 0.35 |
| Unburnt forest | 0.07 | **0.87** | 0.13 | 0.05 | –0.01 | 0.06 | –0.13 |
| Stream | 0.20 | –0.09 | –0.08 | –0.12 | –0.02 | **0.90** | 0.02 |
| Standing dead burnt trunks | 0.16 | 0.07 | 0.09 | –0.20 | **0.89** | –0.04 | 0.13 |
| Laying dead burnt trunks | –0.32 | –0.10 | 0.18 | 0.39 | **0.70** | 0.03 | –0.20 |
| Eigenvalue | 6.27 | 2.13 | 1.85 | 1.38 | 1.05 | 0.91 | 0.84 |
| % Total variance | 34.86 | 11.81 | 10.30 | 7.69 | 5.83 | 5.07 | 4.64 |

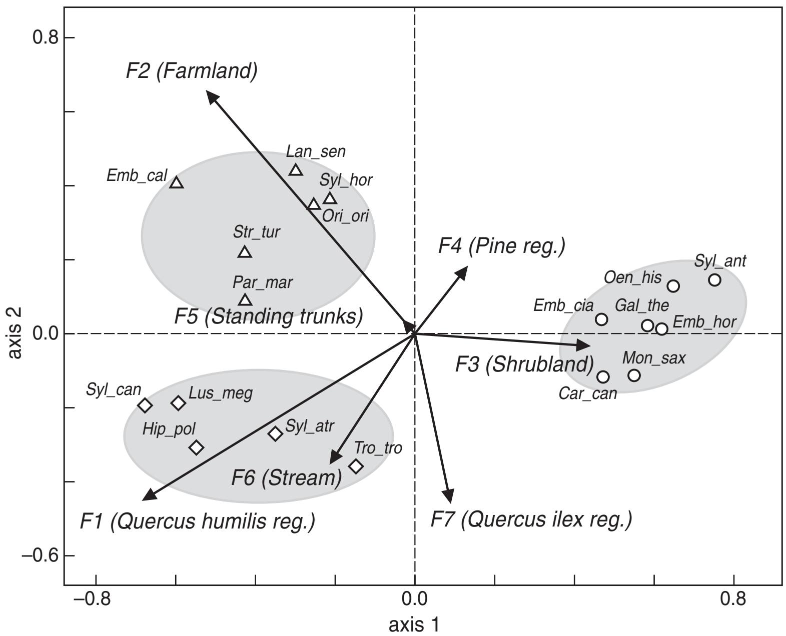


**Figure 2.** Associations estimated between the bird species and the environmental variables by the Redundancy Analysis. Only the bird species that are well characterized by the first two axes are shown. Complete names of the species acronyms are given in Appendix 1.

especially in north-facing slopes, and included the Melodious Warbler *Hippolais polyglotta*, the Subalpine Warbler *Sylvia cantillans* and the Blackcap *Sylvia atricapilla*. The second group described the bird community using burnt mosaic areas prevailing near farmland in which small patches of non-burnt pine forests were still present after the fire, and was characterised by species such as the Turtle Dove *Streptopelia turtur*, the Woodchat Shrike *Lanius senator* and the Golden Oriole *Oriolus oriolus*. Finally, a third group defined open habitat species, using sparse vegetation with very poor or no post-fire tree regeneration, such as the Ortolan Bunting *Emberiza hortulana*, the Tawny Pipit *Anthus campestris* and the Black-eared Wheatear *Oenanthe hispanica*.

In bird specific analysis, we found that 71% of the studied species significantly responded to one of the first three vegetation gradients distinguished in the PCA (Table 2). Whereas the *Q. humilis* regeneration gradient had contradicting effects on different species (9 species responding positively to the gradient and 8 negatively), the farmland gradient had a generally positive effect on many species, with up to 18 species positively affected by this gradient and only 5 negatively related to it (Table 2). Also the shrubland gradient tended to positively influence more species (9) than exert a negative influence (only 3). The regeneration of other trees rather than deciduous oaks, namely pines and Holm Oaks, tended to have strong negative effects on species, with 4 and 7 negatively and only 1 and 1 positively related to pine and Holm Oak respectively. Finally, the presence of specific features such standing dead trunks or streams on the transects tended to have a positive effect on bird abundance, with 5 and 9 positively and only 1 and 1 species negatively related to these two gradients respectively (Table 2).

On the other hand, the Conservation Index of the bird species was significantly related to post-fire regeneration patterns ($F_{7, 92} = 7.06$, $P < 0.0001$). In order to further analyse the possible relation between vegetation patterns and conservation objectives, we considered only those vegetation gradients estimated in the PCA that explained slightly more than 50% of total variation (i.e. F1 (*Q. humilis* regeneration); F2 (Farmland); and F3 (Shrubland)). In this sense, the Conservation Index of the bird species in the burnt area significantly decreased in areas where resprouters of *Q. humilis* dominate ($F_{1, 98} = 25.02$, $P < 0.0001$) and significantly increased in shrubland areas ($F_{1, 98} = 12.32$, $P < 0.001$) (Fig. 3). On the other hand, the Conservation Index of the bird species was not significantly related to the farmland habitat type ($P > 0.05$) (Fig. 3).

**Table 2.** Relationship between bird species and the seven factors obtained by the PCA as tested with generalized linear model and generalized linear mixed models[a].

| Species | *Quercus humilis* reg. | Farmland | Shrubland | Pine reg. | Standing trunks | Stream | *Quercus ilex* reg. | Random factor[b] |
|---|---|---|---|---|---|---|---|---|
| Red-legged Partridge *Alectoris rufa* | | | | | | | | ns |
| Common Wood Pigeon *Columba palumbus* | | +++ | | | | | | ns |
| European Turtle Dove *Streptopelia turtur* | | +++ | | | | | | ** |
| Common Cuckoo *Cuculus canorus* | | | | | | | | ns |
| Eurasian Hoopoe *Upupa epops* | | ++ | | | | | | ns |
| Eurasian Wryneck *Jynx torquilla* | | | | | | | + | ns |
| European Green Woodpecker *Picus viridis* | + | | | | +++ | | | ns |
| Great Spotted Woodpecker *Dendrocopos major* | | | | | | | | ns |
| Thekla Lark *Galerida theklae* | | | | | | | | ** |
| Crested Lark *Galerida cristata* | | + | | | | | – | ns |
| Woodlark *Lullula arborea* | | | | | | | | ns |
| Eurasian Skylark *Alauda arvensis* | | | | | | | | ns |
| Tawny Pipit *Anthus campestris* | – | | | | | | | ns |
| Winter Wren *Troglodytes troglodytes* | | | | | | +++ | | ns |
| Thrush Nightingale *Luscinia megarhynchos* | +++ | +++ | | – | | +++ | | * |
| European Stonechat *Saxicola torquata* | – | | | | | | | ns |
| Black-eared Wheatear *Oenanthe hispanica* | ––– | – | +++ | | | | | ** |
| Rock Thrush *Monticola saxatilis* | ––– | ––– | ++ | – | | | | ** |
| Common Blackbird *Turdus merula* | | ++ | | | | ++ | | * |
| Melodious Warbler *Hippolais polyglotta* | +++ | | ––– | – | | +++ | | ** |
| Dartford Warbler *Sylvia undata* | ––– | ––– | +++ | | | | – | ** |
| Subalpine Warbler *Sylvia cantillans* | +++ | ++ | | | | | | ** |
| Sardinian Warbler *Sylvia melanocephala* | | | | | | + | ––– | * |
| Western Orphean Warbler *Sylvia hortensis* | | +++ | | | | | | ns |
| Eurasian Blackcap *Sylvia atricapilla* | +++ | | | ––– | + | +++ | | * |
| Western Bonelli's Warbler *Phylloscopus bonelli* | + | +++ | | | | + | | ** |
| Long-tailed Bushtit *Aegithalos caudatus* | | | | | + | ++ | | ns |
| European Crested Tit *Lophophanes cristatus* | | | + | +++ | ++ | ––– | | * |
| European Blue Tit *Cyanistes caeruleus* | +++ | + | + | | | | | ns |
| Great Tit *Parus major* | ++ | ++ | | | | | | * |
| Eurasian Golden Oriole *Oriolus oriolus* | | +++ | | | | | | ** |
| Great Grey Shrike *Lanius meridionalis* | | | | | + | | | ns |
| Woodchat Shrike *Lanius senator* | | +++ | | | | | – | * |
| Eurasian Jay *Garrulus glandarius* | | | ++ | | | | | ** |
| Carrion Crow *Corvus corone* | | ++ | | | | | | ns |
| Common Starling *Sturnus vulgaris* | | + | | | | | ––– | ns |
| Rock Sparrow *Petronia petronia* | | | | | | + | –– | ns |
| Common Chaffinch *Fringilla coelebs* | | +++ | | | | | | ns |
| European Serin *Serinus serinus* | | | | | | | | * |
| European Goldfinch *Carduelis carduelis* | | | –– | | | | | ns |
| Common Linnet *Carduelis cannabina* | – | –– | + | | | | | ** |
| Cirl Bunting *Emberiza cirlus* | | ++ | | | | | | * |
| Rock Bunting *Emberiza cia* | – | | + | | | | | ** |
| Ortolan Bunting *Emberiza hortulana* | ––– | – | + | | – | | | ** |
| Corn Bunting *Emberiza calandra* | ++ | +++ | ––– | | | | ––– | ** |

[a]Negative relationships: (–) $P < 0.05$, (––) $P < 0.01$, (–––) $P < 0.001$; positive relationships: (+) $P < 0.05$, (++) $P < 0.01$, (+++) $P < 0.001$.
[b]Analysis of the site effect on species distribution: ns (not significant), * ($P < 0.05$), ** ($P < 0.01$).

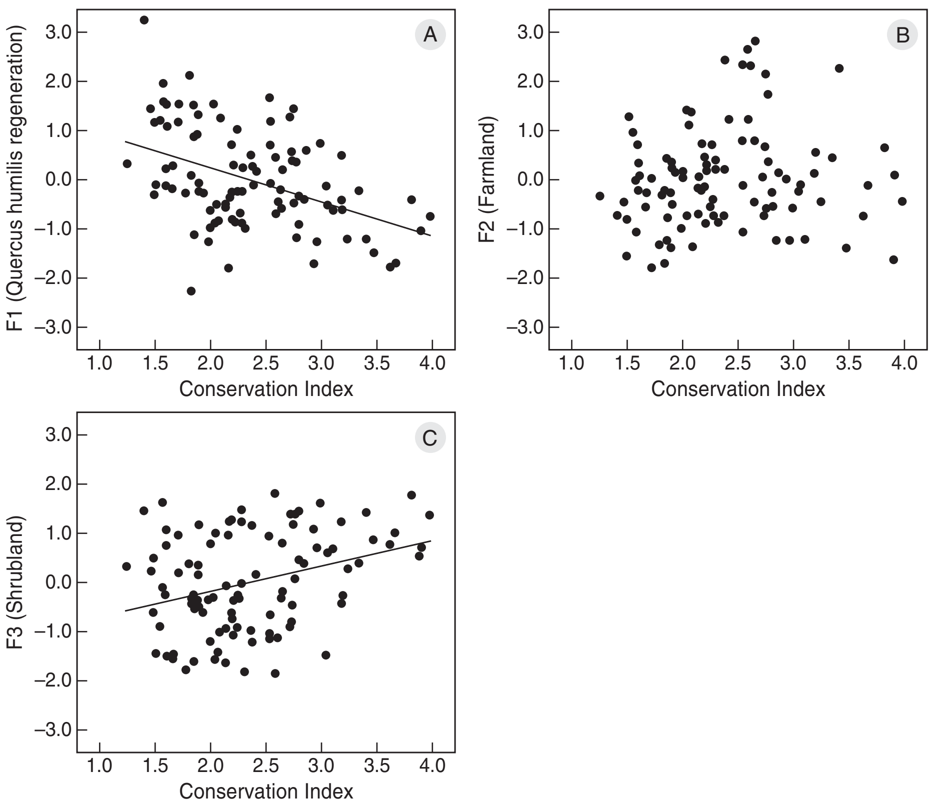


**Figure 3.** Relationship between bird Conservation Index and the main factors describing vegetation recovery obtained by the PCA. (A) *Quercus humilis* regeneration ($P < 0.01$), (B) Farmland (n.s.), (C) Shrubland ($P < 0.01$).

## DISCUSSION

With this work, we have shown that bird communities strongly respond to post-fire heterogeneity in vegetation recovery after fire. Landscape heterogeneity arising from variable patterns of vegetation regeneration creates a mosaic of suitable habitats for bird species with different habitat requirements. From the conservation point of view, the open habitats originating in areas where non-tree regeneration takes place leading to areas dominated by open shrub lands are of particular importance.

Bird species respond to changes in habitat structure and composition such as those generated after fire (e.g. Prodon & Lebreton 1981, Hobson & Schieck 1999, Brawn *et al.* 2001). In the Mediterranean region, landscapes are assumed to be highly resilient to fire (Trabaud & Lepart 1980, Lloret *et al.* 1999). Thus, depending on the vegetation type bird composition and richness can recover after 1 year in dry grassland, some 15 years in a Cork Oak *Quercus suber* forest, and probably around one century in a mature Evergreen Oak *Quercus ilex* forest (Prodon *et al.* 1984, Prodon 1988, Jacquet & Prodon 2009). However, in cases in which ecosystems do not return to pre-fire conditions such as in *Pinus nigra* forests, post-fire environmental conditions are expected to determine bird structure inducing important changes in bird composition and richness. In this study we analyzed, for the first time, the bird community found 7 years after a large fire that affected a *Pinus nigra* forested area. Our results have shown that the post-fire bird community is strongly associated with vegetation recovery, even when strong vegetation changes occurred due to non-direct regeneration of dominant forest tree species after a large fire.

The new mosaic of habitats created 7 years after fire facilitates the appearance of a large variety of bird species matching the main regeneration patterns. This result is in agreement with previous studies suggesting that habitat heterogeneity at the local scale enhances the occurrence of a rich bird community (Dunning *et al.* 1992, Brotons *et al.* 2005). This association between spatial heterogeneity and bird richness has been repeatedly reported (Wiens 1989). In our case, we found three main landscape gradients determining spatial variability of bird community structure. The principal one showed the incipient formation of a new forest dominated by young resprouters of *Q. humilis* prevailing mainly in the north-facing slopes (Espelta *et al.* 2003). In this habitat we found a low number of specialist bird species, mainly undergrowth species, such as the Blackcap and the Subalpine Warbler. These species find trophic resources, breeding sites and refuge within the stands. A mature stage of this forest type would favour species preferring canopy cover such as the Bonelli's Warbler *Phylloscopus bonelli*, enhancing bird richness and abundance (Camprodon & Brotons 2006).

The second main landscape gradient was a mosaic of habitats, where patches of non-burnt forests, burnt areas and agriculture lands coexist. This landscape prevailed in flat areas as the result of the less aggressive behaviour of fire on gentle slopes, together with a more effective impact of fire fighting efforts in more developed and accessible areas. In this mosaic a combination of farmland, shrubland and some forest bird species coexist. Many of the farmland species are species that typically feed in the fields but nest in the edge or in forest patches, such as the Woodlark *Lullula arborea* and the Golden Oriole (Brotons *et al.* 2004). These species benefit from the coexistence of open habitats, as occurring after fire (i.e. farmland and shrublands) (Fuller *et al.* 2004; Vallecillo *et al.* 2008). Forest bird species were present in this mosaic landscape as a consequence of the use of unburnt patches of pine trees left relatively untouched (Herrando *et al.* 2002). However, common forest bird species, such as Short-toed Treecreeper *Certhia brachydactyla*, Firecrest *Regulus ignicapilla* and Chiffchaff *Phylloscopus collybita*, were absent or present in very low numbers after the fire. These species concentrate their activity in the canopy and this habitat was only present in small patches, surrounded by unsuitable farmland or burnt habitat. Although strong site fidelity of forest and shrubland birds after fire has been reported (Pons & Bas 2005), we do not think that this process is likely to explain the presence of these species seven years after the fire. We rather suggest that unburnt forest patches are likely to act as remaining islands of the original pine forest habitats (Brotons *et al.* 2004) and thus host an impoverished forest bird community in which more specialist forest species, such as the Nuthatch *Sitta europaea*, have been lost and others have decreased (Estrada *et al.* 2004).

Other common forest species such as the Wren *Troglodytes troglodytes* and the Nightingale *Luscinia megarhynchos* were positively associated with riparian areas, where vegetation regeneration after fire was rapid but only local along the stream sides. These areas are rich in fruits and invertebrates and many bird species find them to be adequate habitats. In contrast, the presence in certain areas of *P. halepensis* and *Q. ilex* resprouters negatively affected the presence of certain species, such as the Sardinian Warbler *Sylvia melanocephala* and the Blackcap. This could be due to the relatively high density of trees found within these areas. Finally, although the main objective of this study was not to analyze the effect of post-fire management activities on the bird community after a large fire, our results show that leaving trunks within the fire perimeter had more positive than negative effects on the bird community, as shown for the Green Woodpecker *Picus viridis* and the Crested Tit *Parus cristatus*. This result is in agreement with previous work that highlight the importance of standing dead trunks for bird diversity in terms of nest site availability, perching sites and foraging substrates (Hutto 2006).

Finally, low shrubs combined with bare ground and grasslands located in south-facing slopes dominated the third main landscape gradient. In these areas, pre-fire abundance of resprouters was low, most likely due to the historical impact of agriculture and/or grazing (Mosandl & Kleinert 1998, Gomez 2003), leading to poor tree vegetation recovery. This habitat provides an adequate environment for a number of shrubland bird species, such as Ortolan Bunting or Tawny Pipit (Menz *et al.* 2009). This habitat, arising from the lack of tree regeneration, is especially relevant since most of the species inhabiting such open habitats are among the most threatened species in Europe (BirdLife International 2004). This was corroborated by our results. The significant positive relation between the species associated with this habitat type and their conservation value highlights the important role of open habitats for species conservation. Several studies have shown the use of recently burnt areas by these species (Herrando *et al.* 2002, Brotons *et al.* 2005, Pons & Bas 2005), however as vegetation succession takes place these species tend to disappear (Prodon *et al.* 1987). The findings of our study have interesting implications for bird conservation in Mediterranean areas since the persistence of open-habitat species seven years after the fire suggests that a non-direct regeneration process might create the appropriate habitat for their conservation.

**Management implications**

Perhaps unsurprisingly, the mosaic of habitats arising after fire has been shown to promote a rich and diverse bird community (Blondel & Aronson 1999, Brotons *et al.* 2004). Although the impact of fire is thought to disappear in later succession stages as vegetation recovers, non-direct regeneration processes as described in the present study or those resulting from repeated fire impact (Díaz-Delgado *et al.* 2002) may lead to the large temporal maintenance or increase of habitat suitable for species linked to open vegetation (Brotons *et al.* 2008). Here, management should be undertaken in order to maintain the new heterogeneous landscape and conserve an important number of species that are considerably declining elsewhere in Europe. In addition, maintenance of heterogeneous landscapes might prevent large and catastrophic wildfires (Lloret *et al.* 2002).

In order to preserve bird diversity in low shrubland landscape, prescribed burning and/or grazing by large herbivores or livestock farming should be considered (Pons *et al.* 2003). Controlled burning is now a widely used management tool that can help at the same time to prevent large-scale catastrophic wildfires (Hardy & Arno 1996, Miller & Urban 2000). Additionally, bird species associated with farmland areas might be favoured by traditional farming (Casals *et al.* 2007). In view of a trend towards land abandonment, compensatory payments to farmers should be provided to maintain traditional farming methods.

On the other hand, thinning would be recommended in areas where forest regenerates (*Q. humilis*, *Q. ilex* and *P. halepensis*) to enhance the growth of remaining trees and favour the presence of forest bird species in these areas while reducing the fire risk associated with dense stands (Gonzalez *et al.* 2006). Regenerating oak stands are especially important since they may lead to forest habitats more resilient to fires (Moreira *et al.* 2001, Díaz-Delgado *et al.* 2002).

Overall, the results of this study suggest that landscape changes induced by non-direct tree regeneration after fire might be viewed as offering promising management opportunities for the conservation of many species. The low rate of vegetation recovery under non-direct tree regeneration leads to long term availability of suitable habitats for bird species under conservation concern associated with low shrubland and farmland habitat. This may halt the general decreasing trend of many of these species in large areas of the Mediterranean region associated with land abandonment processes prevailing in the last 40 years (Sirami *et al.* 2007).

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## SAMENVATTING

Er komen in het Middellandse Zeegebied veelvuldig bosbranden voor. De gevolgen van deze branden zijn meestal maar kortstondig, doordat de bossen zich snel herstellen. In de weinige gevallen dat volledig herstel uitblijft, kunnen echter grote veranderingen in het landschap optreden, doordat er dan een lappendeken ontstaat van plekken die wel en niet zijn hersteld. Het onderhavige onderzoek richtte zich op de vraag in hoeverre dergelijke veranderingen in het landschap de vogelbevolking beïnvloeden. Daartoe werden waarnemingen verzameld in het midden van Catalonië in het noordoosten van Spanje, waar tijdens een brand in 1998 26.000 ha land, hoofdzakelijk bestaande uit naaldbossen (Zwarte Den *Pinus nigra*) en graanakkers, verwoest werd. Zeven jaar na de brand werden het landschap en de vegetaties in detail beschreven, in combinatie met lijntransectonderzoek naar de talrijkheid van vogels. De verspreiding en dichtheid van vogels was voor ruim 31% te verklaren uit de nieuw ontstane patronen in het landschap. De vogels waren in verschillende groepen te rangschikken afhankelijk van hun binding aan drie landschaptypes: (1) herstellende eikenbossen, (2) de nabijheid van akkerland met pijnboomopstanden die aan de brand waren ontsnapt, (3) kale, nog niet herstelde plekken. Er bestond een sterk verband tussen het voorkomen van de verschillende vogelsoorten en gradiënten in de vegetatie. De natuurwaardes van de vogelbevolking was het laagst in gebieden met uitlopende Donseik *Quercus humilis* en het hoogst op hellingen die met lage struiken waren begroeid. Het onderzoek laat zien dat, afhankelijk van het type bos, bosbranden een volledig nieuw landschap tot gevolg kunnen hebben met mogelijkheden voor vogelsoorten die worden bedreigd in Europa. (JS)

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**Appendix 1.** List of bird species found in the study area showing the conservation status according to the indices of the EU Birds Directive (70/409/CEE); the highest abundance of both visits carried out in the field survey (number of bird individuals seen or heard) and percentage of transects occupied by each species (occurrence).

| Species | Acronym | Conservation status | Abundance | Occurrence (%) |
|---|---|---|---|---|
| Red-legged Partridge *Alectoris rufa* | Ale_ruf | SPEC 2 | 85 | 50 |
| Common Quail *Coturnix coturnix* | Cot_cot | SPEC 3 | 4 | 4 |
| Common Wood Pigeon *Columba palumbus* | Col_pal | Non-SPEC | 48 | 34 |
| European Turtle Dove *Streptopelia turtur* | Str_tur | SPEC 3 | 54 | 35 |
| Common Cuckoo *Cuculus canorus* | Cuc_can | Non-SPEC | 13 | 13 |
| European Nightjar *Caprimulgus europaeus* | Cap_eur | SPEC 2 | 2 | 2 |
| European Roller *Coracias garrulus* | Cor_gar | SPEC 2 | 1 | 1 |
| Eurasian Hoopoe *Upupa epops* | Upu_epo | SPEC 3 | 13 | 10 |
| Eurasian Wryneck *Jynx torquilla* | Jyn_tor | SPEC 3 | 24 | 22 |
| European Green Woodpecker *Picus viridis* | Pic_vir | SPEC 2 | 14 | 12 |
| Great Spotted Woodpecker *Dendrocopos major* | Den_maj | Non-SPEC | 32 | 27 |
| Thekla Lark *Galerida theklae* | Gal_the | SPEC 3 | 19 | 14 |
| Crested Lark *Galerida cristata* | Gal_cri | SPEC 3 | 6 | 6 |
| Woodlark *Lullula arborea* | Lul_arb | SPEC 2 | 246 | 91 |
| Eurasian Skylark *Alauda arvensis* | Ala_arv | SPEC 3 | 10 | 10 |
| Tawny Pipit *Anthus campestris* | Ant_cam | SPEC 3 | 17 | 17 |
| White Wagtail *Motacilla alba* | Mot_alb | Non-SPEC | 1 | 1 |
| Winter Wren *Troglodytes troglodytes* | Tro_tro | Non-SPEC | 30 | 26 |
| European Robin *Erithacus rubecula* | Eri_rub | Non-SPEC | 3 | 3 |
| Thrush Nightingale *Luscinia megarhynchos* | Lus_meg | Non-SPEC | 166 | 75 |
| Whinchat *Saxicola rubetra* | Sax_rub | Non-SPEC | 2 | 2 |
| European Stonechat *Saxicola torquatus* | Sax_tor | Non-SPEC | 172 | 80 |
| Black-eared Wheatear *Oenanthe hispanica* | Oen_his | SPEC 2 | 76 | 39 |
| Northern Wheatear *Oenanthe oenanthe* | Oen-oen | SPEC 3 | 1 | 1 |
| Rock Thrush *Monticola saxatilis* | Mon_sax | SPEC 3 | 43 | 30 |
| Blue-Rock Trush *Monticola solitarius* | Mon_sol | SPEC 3 | 4 | 4 |
| Common Blackbird *Turdus merula* | Tur_mer | Non-SPEC | 56 | 48 |
| Mistle Thrush *Turdus viscivorus* | Tur_vis | Non-SPEC | 1 | 1 |
| Song Thrush *Turdus philomelos* | Tur_phi | Non-SPEC | 1 | 1 |
| Cetti's Warbler *Cettia cetti* | Cet_cet | Non-SPEC | 1 | 1 |
| Great Reed Warbler *Acrocephalus arundinaceus* | Acr_aru | Non-SPEC | 1 | 1 |
| Melodious Warbler *Hippolais polyglotta* | Hip_pol | Non-SPEC | 134 | 58 |
| Dartford Warbler *Sylvia undata* | Syl_und | SPEC 2 | 355 | 80 |
| Subalpine Warbler *Sylvia cantillans* | Syl_can | Non-SPEC | 363 | 90 |
| Sardinian Warbler *Sylvia melanocephala* | Syl_mel | Non-SPEC | 44 | 32 |
| Western Orphean Warbler *Sylvia hortensis* | Syl_hor | SPEC 3 | 18 | 17 |
| Eurasian Blackcap *Sylvia atricapilla* | Syl_atr | Non-SPEC | 30 | 23 |
| Garden Warbler *Sylvia borin* | Syl_bor | Non-SPEC | 1 | 1 |
| Common Whitethroat *Sylvia communis* | Syl_com | Non-SPEC | 3 | 3 |
| Bonelli's Warbler *Phylloscopus bonelli* | Phy_bon | SPEC 2 | 53 | 38 |
| Spotted Flycatcher *Muscicapa striata* | Mus_str | SPEC 3 | 2 | 2 |
| Long-tailed Tit *Aegithalos caudatus* | Aeg_cau | Non-SPEC | 18 | 9 |
| European Crested Tit *Parus cristatus* | Par_cri | SPEC 2 | 12 | 9 |
| European Blue Tit *Parus caeruleus* | Par_cae | Non-SPEC | 13 | 10 |
| Great Tit *Parus major* | Par_maj | Non-SPEC | 89 | 56 |

**Appendix 1.** Continued

| Species | Acronym | Conservation status | Abundance | Occurrence (%) |
|---|---|---|---|---|
| Short-toed Treecreeper *Certhia brachydactyla* | Cer_bra | Non-SPEC | 3 | 3 |
| Eurasian Golden Oriole *Oriolus oriolus* | Ori_ori | Non-SPEC | 35 | 25 |
| Great Grey Shrike *Lanius meridionalis* | Lan_mer | SPEC 3 | 62 | 49 |
| Woodchat Shrike *Lanius senator* | Lan_sen | SPEC 2 | 35 | 26 |
| Eurasian Jay *Garrulus glandarius* | Gar_gla | Non-SPEC | 44 | 33 |
| Common Raven *Corvus corax* | Cor_corax | Non-SPEC | 4 | 2 |
| Carrion Crow *Corvus corone* | Cor_cor | Non-SPEC | 15 | 12 |
| Common Starling *Sturnus vulgaris* | Stu_vul | SPEC 3 | 18 | 11 |
| Rock Sparrow *Petronia petronia* | Pet_pet | Non-SPEC | 27 | 9 |
| Common Chaffinch *Fringilla coelebs* | Fri_coe | Non-SPEC | 8 | 7 |
| European Serin *Serinus serinus* | Ser_ser | Non-SPEC | 69 | 47 |
| European Greenfinch *Carduelis Chloris* | Car_chl | Non-SPEC | 1 | 1 |
| European Goldfinch *Carduelis carduelis* | Car_car | Non-SPEC | 23 | 14 |
| Common Linnet *Carduelis cannabina* | Car_can | SPEC 2 | 297 | 83 |
| Cirl Bunting *Emberiza cirlus* | Emb_cir | Non-SPEC | 85 | 51 |
| Rock Bunting *Emberiza cia* | Emb_cia | SPEC 3 | 227 | 87 |
| Ortolan Bunting *Emberiza hortulana* | Emb_hor | SPEC 2 | 155 | 61 |
| Corn Bunting *Emberiza calandra* | Emb_cal | SPEC 2 | 239 | 76 |