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# Time-window of occurrence and vegetation cover preferences of Dartford and Sardinian Warblers after fire

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**Abstract** Wildfires are the most extensive and severe disturbance affecting the shrublands where Sardinian and Dartford Warblers (*Sylvia melanocephala* and *S. undata*) abound. Estimating the long-term use of burned habitats by these species (i.e. their time-window of occurrence) is fundamental to understanding their regional distribution and to plan possible conservation measures for the near-threatened Dartford Warbler. In this study, we describe the post-fire time-window of occurrence and cover preferences of the two warblers using an abundance dataset, gathered by point counts over 22 consecutive years, and a density dataset, resulting from territory mapping of four different plots for up to 8 years. Both datasets span before and after fire. The two species colonized burned areas as soon as the second year after fire. The Dartford Warbler showed its highest abundance between 4 and 9 years after fire and

disappeared after 16 years or more. The Sardinian Warbler had a peak of abundance at 9 years, but the study was not long enough to record its local extinction. Partial least squares regression showed that abundance at points and plot density of the Dartford Warbler were positively related to the plant cover between 0.25 and 1 m, whereas vegetation between 0.5 and 4 m was important for the Sardinian Warbler. The Dartford Warbler, therefore, depends on the existence of dense and low shrublands, that are often the result of past fires.

**Keywords** *Sylvia* warblers Mediterranean shrublands Ecological succession Vegetation structure Fire ecology Mapping method Point counts

## Zusammenfassung

Zeitliches Auftreten und Vegetationspräferenzen von Provencegrasmücke und Samtkopf-Grasmücke nach Flächenbränden

Flächenbrände stellen die großräumigsten und tiefsten Einschnitte in den Buschland-Habitaten dar, in denen Samtkopf-Grasmücke (*Sylvia melanocephala*) und Provencegrasmücke (*Sylvia undata*) vorkommen. Eine Einschätzung der langfristigen Nutzung der abgebrannten Lebensräume durch diese Arten (d. h. das Zeitfenster ihres Vorkommens) ist von grundlegender Bedeutung für das Verständnis ihrer räumlichen Verteilung und bei der Planung möglicher Schutzmaßnahmen für die als “gering gefährdet” eingestufte Provencegrasmücke. Diese Studie beschreibt das Zeitfenster des Auftretens nach dem Brand und die Vegetationspräferenzen der zwei Grasmückenarten auf der Grundlage von Häufigkeitsdaten aus 22 aufeinander folgenden Jahren mit Punktzählungen und von Dichtedaten

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aus einer Flächenkartierung in vier verschiedenen Gebieten über bis zu acht Jahren. Beide Datensätze umfassen die Zeit vor und nach einem Brand. Beide Arten besiedelten verbrannte Flächen bereits im zweiten Jahr nach dem Feuer. Die Provencegrasmücke zeigte ihre höchste Bestandsdichte zwischen vier und neun Jahren nach einem Brand und verschwand nach 16 oder mehr Jahren. Die Samtkopf-Grasmücke erreichte ihre größte Häufigkeit nach neun Jahren, die Laufzeit der Studie war jedoch nicht lang genug, um ihr lokales Aussterben zu dokumentieren. Die Partial Least Squares Pfadanalyse zeigte, dass bei der Provencegrasmücke die Häufigkeit an den Zählpunkten sowie die Flächendichte positiv mit einer Bodenbewuchshöhe zwischen 0,25 und 1 m korrelierten, wohingegen für die Samtkopf-Grasmücke Vegetationshöhen zwischen 0,5 und 4 m von Bedeutung waren. Die Provencegrasmücke ist daher stärker vom Vorhandensein dichten und niedrigen Gebüschs abhängig, wie es häufig nach Bränden entsteht.

## Introduction

Land use changes and ecological disturbances are the main drivers of landscape dynamics. Typical disturbances in forest ecosystems include logging, fire, floods, severe droughts, windstorms, snow avalanches, landslides, and insect outbreaks (White and Pickett 1985; Attiwill 1994). All of them result in a simplification of the habitat structure that usually favors open-habitat bird species (Wiens 1989). Thereafter, cover regeneration tends to benefit shrubland first, then forest species (Brawn et al. 2001). Colonization, which requires dispersal followed by successful establishment, and local extinction determine the temporal occurrence of individual species in ecological successions. Therefore, for many species, excluding extreme habitat generalists, it seems possible to identify a time-window along the succession in which animals occur and breed. Species time-windows will be variable between sites, due to the severity of the disturbance and to habitat resilience, among others, but some general patterns can be identified (Watson et al. 2012). In the Mediterranean Basin, wildfires are often considered the ‘major’ disturbance in terms of extension, severity, and recurrence (Pausas et al. 2008), and their impact is predicted to increase with climate warming (Piñol et al. 1998). Estimating species time-windows of occurrence after large fires is thus important in understanding the regional distribution of species and in planning effective conservation measures. However, exploring these temporal patterns is not easy, since long-term diachronic studies or a difficult reconstruction of succession from several study sites burned at different dates are required (Prodon and Pons 1993).

Most *Sylvia* warblers are mid-successional insectivorous passerines frequent in post-disturbance shrubland. Up to 8 *Sylvia* species, from the 26 currently recognised, can breed sympatrically, although usually no more than 4 or 5 share the same habitat (Glutz von Blotzheim and Bauer 1991; Shirihai et al. 2001). When Mediterranean species do occur syntopically, they segregate more by foraging microhabitat use than by territorial exclusion (Martin and Thibault 1996; Pons et al. 2008). Two of these species, the Sardinian Warbler (*Sylvia melanocephala*) and the Dartford Warbler (*Sylvia undata*), are often found in recently burned areas.

The Sardinian Warbler has a peri-Mediterranean breeding distribution that extends southwest from northern Africa to the Canary Islands. It favors Mediterranean climate areas, where it can be one of the most common species in shrublands and forests. This species is globally evaluated as Least Concern in the IUCN Red List, since it has a very large range and population size, and since its population trend appears to be increasing (BirdLife International 2011). It is particularly abundant in tall shrublands and in open forests with a dense understory (Glutz von Blotzheim and Bauer 1991; Shirihai et al. 2001). The Dartford Warbler, for its part, is patchily distributed in shrublands of south-western Europe and north-western Africa. Its global conservation status was uplisted in 2008 to the Near Threatened (NT) category, based on an estimated population decline of 27% during 1990–2005 (BirdLife International 2011). The causes of the decline are not clear but seem related to land use changes and habitat degradation in its core population in Spain. Wildfires and changes in the fire regime have been cited among the major threats to this warbler (Tucker and Heath 1994), although several authors have shown that the species is abundant in burned areas of France, Spain, and Portugal (Pons and Prodon 1996; Herrando et al. 2001; Moreira et al. 2003). Although the bulk of the Dartford Warbler population and roughly 70% of its breeding range lie in a Mediterranean climate (BirdLife International 2011), most Dartford warbler ecological studies have been carried out in the small and peripheral English population (Bibby 1979; Catchpole and Phillips 1992; van den Berg et al. 2001; Murison et al. 2007), which faces a different environment, climate and threats than the Mediterranean populations. It is therefore essential to improve our knowledge of the species biology in its core range.

The main objective of this study is to describe post-fire time-windows of occurrence in the Dartford and Sardinian Warblers in burned habitats in their core breeding range. Furthermore, we aimed to relate the species’ abundances to habitat structure and time since fire. To this aim, we used several shrubland plots that were studied after fire (one plot) or before and after fire (three plots). We also used several point count stations, in the vicinity of one of the plots, which were studied in the long term (1983–2004).

## Methods

## Study area

The study was conducted in Catalonia, a core region in the distribution of the genus *Sylvia* (Shirihai et al. 2001). Four plots were located, from north to south, at Torderes (TO) and Err (ER) in France, and at La Jonquera (LJ) and Torroella de Montgrí (TM) in Spain. TO, LJ, and TM were located in low mountains with a Mediterranean climate, whereas ER was found in the high Pyrenees at subalpine level (Table 1). Plot habitats were representative of common habitats of the study area. Dartford and Sardinian Warblers are widely distributed in this area, except in the mountains around ER where the Dartford Warbler is scarce and the Sardinian Warbler absent. Plot vegetation was affected by wildfire (LJ and TM) or by prescribed burning (TO and ER), before (LJ) or during the course of the study (the three other plots). Once burned, the plots were mildly managed (light cattle grazing in ER, light sheep grazing in TO, selective logging 3–4 years after the fire in TM) or not managed at all (LJ). Moreover, 11 sampling stations for long-term point counts were

located in the vicinity of the LJ plot and in the same habitat (young cork oak forest).

## Vegetation structure and bird density

At the start of the study, the habitat at TO was a 15-year-old post-fire shrubland with an average shrub height of 1.5 m. LJ consisted of a young cork oak forest with an 8-m canopy and a well-developed undergrowth. TM was more heterogeneous, although dominated by 0.2- to 2-m shrubs with a variable density of pines, its vegetation having developed after land abandonment that occurred some 38 years ago. ER was a 35-year-old dense shrubland with a low density of young pines. The main plant species are shown in Table 1. Plot vegetation was severely burned by wildfires at LJ and TM, resulting in extensive and rapid regrowth. In contrast, patchy prescribed burning turned the shrubland of the other plots into a mosaic of unburned and regenerating burned patches. Thereafter, the vegetation regenerated more slowly in the subalpine plot than in the Mediterranean one. We measured vegetation structure once a year during bird breeding season at fixed sites, regularly distributed at  $\approx 100$ -m intervals, on every plot (10–16 or

study plots	LJ	TO	TM	ER
Locality	La Jonquera	Torderes	Torroella Montgrí	Err
Latitude	42825 <sup>h</sup> N	42834 <sup>h</sup> N	42805 <sup>h</sup> N	42826 <sup>h</sup> N
Longitude	2854 <sup>h</sup> E	2845 <sup>h</sup> E	3811 <sup>h</sup> E	2804 <sup>h</sup> E
Altitude a.s.l.	240 m	290 m	105 m	1,900–2,100 m
Substrate	Granite	Schistous	Limestone	Schistous
Mean annual rainfall	844 mm	776 mm	630 mm	703 mm
Mean annual temp.	14.3°C	14.1°C	15.1°C	5.0°C
Main grass species	Brachypodium retusum	Brachypodium retusum	Brachypodium retusum	Festuca paniculata
Main shrub species	Erica arborea Cistus monspeliensis Ulex parviflorus	Erica arborea Cistus monspeliensis Ulex parviflorus	Quercus coccifera Rosmarinus officinalis Cistus albidus	Cytisus balansae Rosa canina Juniperus communis
Main tree species	Calycotome spinosa Quercus suber	Quercus coccifera Quercus suber	Pinus halepensis	Pinus uncinata
Prefire tree density	512 trees/ha	5 trees/ha	27 trees/ha	17 trees/ha
Plot side length	400 $\times$ 400 m	300 $\times$ 275 m	350 $\times$ 350 m	333 $\times$ 300 m
Plot area	16 ha	8.25 ha	12.25 ha	10 ha
Plot area burned	100%	76%	89%	88%
Fire extent	29,800 ha	12 ha	374 ha	25 ha
Fire date	July 1986	March 1993	June 2001	November 1997
Years studied	1987–1994	1991–1996, 1998	1997–1999, 2002–2005	1997–2000

17–19 sites/10 ha in homogeneous or heterogeneous cover, respectively). Each sampling site covered an area of  $\approx 1,200 \text{ m}^2$ , in which the foliage cover (the projection of the foliage volume of the layer onto a horizontal plane; in %) of five vegetation layers (0–0.25 m, 0.25–0.5 m, 0.5–1 m, 1–2 m, and 2–4 m) was estimated by comparison with a template (Prodon and Lebreton 1981).

Breeding birds were censused between 1987 and 2005, for sampling periods spanning 3–8 years after the fire and, in three plots, 1–3 years before the fire, totalising 26 plot-years. We used the mapping method (IBCC 1969), known as spot-mapping in North America, which produces detailed maps of the breeding territories of territorial birds occurring in a plot. Although time consuming, this method allows a reasonable estimation of absolute densities, provided that focal species show conspicuous territorial behavior (Bibby et al. 1997), as happens with most passerines including *Sylvia* warblers. Moreover, the method allows small areas to be studied and fine-scale habitat associations to be made (Sutherland et al. 2004). An effort was made to standardise the mapping procedure among observers (P.P., J.M.B., and R.P.), including field training and map interpretation. We concentrated on simultaneous singing in order to distinguish between neighboring territorial males. Observations from daily visits in May and June were accumulated until there was little doubt about the location of territory boundaries. The final number of visits ranged from 4 to 16 per year, depending on plot size, vegetation structure and bird density. Mapping fieldwork totaled around 1,200 h. Plot density (breeding pairs/10 ha) was calculated taking into account not only territories totally included in the plot but also the within-plot proportion (0–0.25–0.5–0.75–1) of edge territories (i.e. those extending outside the plot).

#### Point counts

We conducted an unlimited distance point count lasting 20 min at each sampling station of LJ study area. Counts were conducted in mornings (before 1100 hours) with no strong wind or rainfall, recording the number of birds seen or heard (hereafter point count data). After the count, we measured the vegetation structure (one measurement/station and year) with the same method and variables used for the plots. This bird–vegetation sampling was performed over 22 consecutive breeding seasons by a single observer (R.P.), 4 before the wildfire occurring in 1986 and 18 afterwards. However, not all stations were sampled every year (5–7 point counts/year, mean = 6.0).

#### Data analyses

Territorial *Sylvia* warbler densities were plotted against time since fire at the four plots. Due to the strong

environmental and ecological differences of ER, we performed the following analyses only with the three Mediterranean plots. The combination of two population measurements (point count data and plot density) with two focal species (Dartford and Sardinian Warblers) resulted in four response variables. Factors affecting these four variables were analyzed by partial least squares regression (PLSR) using Statistica. The explanatory variables used were the foliage cover (in %) of the five vegetation layers defined above, and the log-transformed time since fire (in years). PLSR combines features of multiple regression and principal components analysis (PCA) (Abdi 2003). It searches for a set of components, called latent vectors, that maximize the covariation between the predictor dataset and the dependent variable. As in a PCA, the vectors are interpreted through the weights of the original variables. The strength of the relationships between each explanatory variable and the dependent variable can be evaluated through scaled regression coefficients ( $b$ ), which range from  $-1$  to  $1$ , being equivalent to regression coefficients in multiple regression analyses. PLSR is especially suitable when predictors are highly correlated and when sample size approaches the number of independent variables. It can provide more reliable results than running a PCA followed by multiple regression (Carrascal et al. 2009).

PLSR does not account for possible unimodal responses, nor for the effect of possible confounding factors (e.g., different study sites). In order to identify possible unimodal responses (a widespread pattern along successions), the relationships between the four warbler response variables and the five cover values were explored individually. Plot data were analyzed with linear mixed models (LMM), using study site as a random factor, while point count data were analyzed with linear models (LM), since they were located in a single study site. We first tested a quadratic relationship (quadratic cover vs. point count data or plot density); if the quadratic term was not significant, we deleted it from the model and tested a linear relationship.

We finally correlated the densities from the LJ plot and the abundances from nearby contemporary point counts to assess whether data obtained using either method were comparable. To achieve this aim, we compared the eight first years after the 1986 fire using Pearson's correlation coefficient with log-transformed variables, when necessary, to improve assumptions of parametric statistics.

#### Results

The 22-year study at LJ cork oak forest showed that foliage cover exceeded pre-fire values after only 2–13 years after fire, depending on the vegetation layer concerned. Lower layers reached the highest cover earlier than the highest

layers, decreasing afterwards (Fig. 1). Point counts showed that only the Sardinian Warbler occurred in the young cork oak forest before the fire. Both species were absent in the

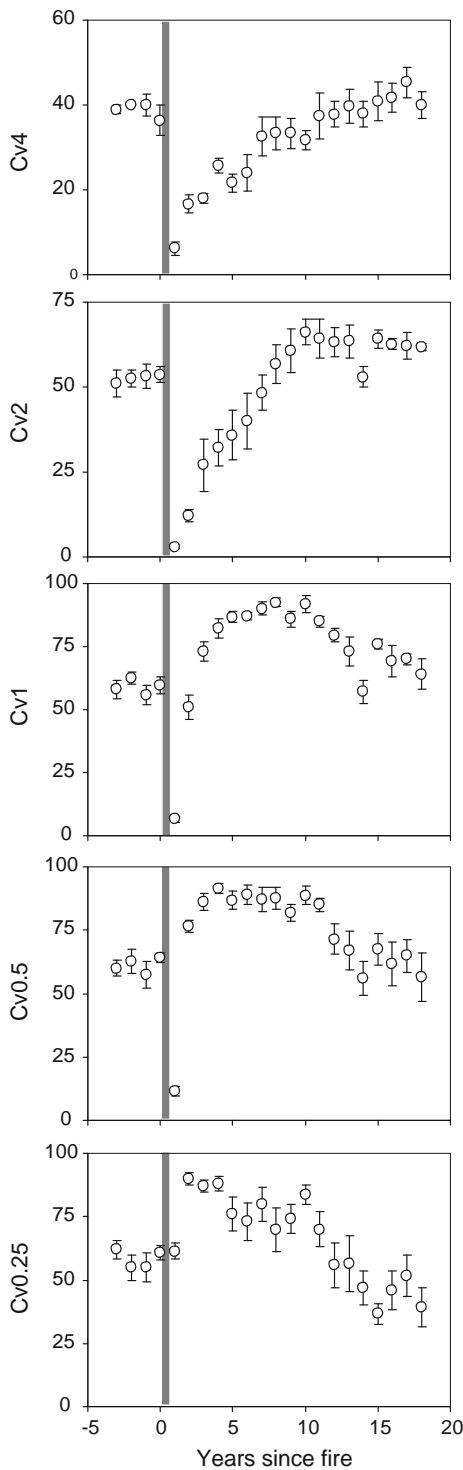


Fig. 1 Changes in foliage cover (in %) of five vegetation layers (2–4, 1–2, 0.5–1, 0.25–0.5 and 0–0.25 m) at the LJ study site from 1983 to 2004, before and after a large wildfire. Error bars show standard error (5–7 stations/year)

first breeding season after fire, but both colonized the area in the second breeding season (Fig. 2). The Sardinian Warbler reached its highest abundance at LJ in the ninth year after fire (4.5 individuals/point count); it decreased afterwards, although it still occurred 18 years after fire. The Dartford Warbler showed two abundance peaks, at 4 and 9 years after fire (1.9 and 2 individuals/point count, respectively), and it occurred until the 15th year after fire.

Compared to pre-fire values, Dartford Warbler plot density dropped by 45, 73, and 80%, respectively in TO, TM, and ER (the three plots that burned incompletely and for which pre-fire assessment was available) in the first breeding season after fire. Density tended to increase with time since fire in two of these plots (not in ER), although the study duration was not sufficient to reveal a unimodal response (Fig. 3). In the completely burned LJ plot, Dartford Warbler density increased sharply from the second year after fire, until it peaked in the fourth year. The Sardinian Warbler showed a similar pattern in LJ and TM, but not in TO, where it was more numerous in the first and sixth years after fire. On the other hand, the Subalpine Warbler (*Sylvia cantillans*) had a fair constant plot density for 8 years after fire in LJ, whereas Common Whitethroat (*Sylvia communis*) disappeared from ER for the three breeding seasons after fire.

In general, bird numbers show a strong relationship with vegetation structure, specifically with low layers for Dartford Warbler, but with intermediate and high layers for Sardinian Warbler. Relationships are, nevertheless, less sharp with time since fire. At the time scale of our study, warbler point count data and plot density showed monotonic (nine significant linear relationships) and unimodal (six significant quadratic relationships) increases with increasing cover of the five vegetation layers (Fig. 4). All vegetation and temporal variables were related to the first or to the second vector of the PLSRs for both species, with

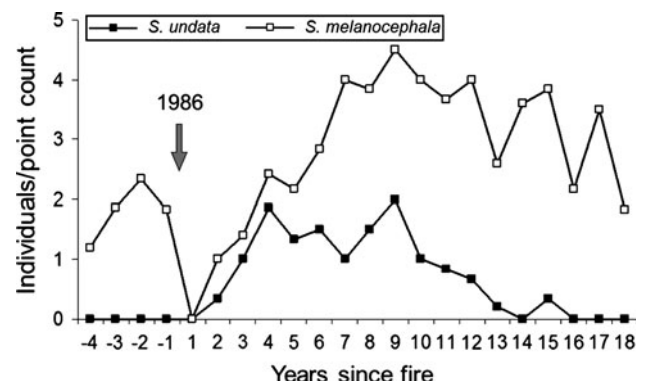


Fig. 2 Mean Dartford (*Sylvia undata*) and Sardinian Warbler (*S. melanocephala*) abundance per point count (5–7 point counts/year) at the LJ study site from 1983 to 2004, before and after a large wildfire (indicated by arrow)



weights of at least 0.45 (in absolute value) for one of the two vectors. The unique exception was the weight of the foliage cover at 0–0.25 m for the PLRS of Sardinian Warbler plot density, which was 0 and –0.15 for the first

and second vector, respectively (Table 2). For the Dartford Warbler, the PLSR coefficients of vegetation layers were rather consistent when comparing point count data and plot density as response variables. In this species, both variables

Fig. 3 Sylvia warbler densities (breeding pairs/10 ha) at the four study plots (LJ, TO, TM, and ER) in relation to time since fire. Arrows show fire occurrence and pie charts the burned area percentage at every plot

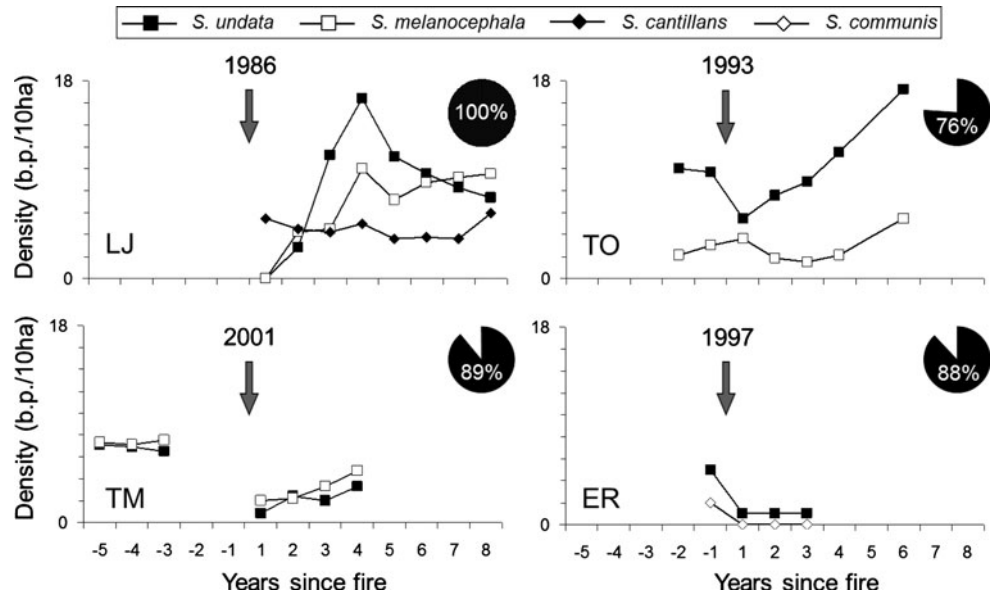


Fig. 4 Relationships between Sylvia warbler point count data (mean number of individuals per point count) and plot density (breeding pairs/10 ha) and habitat variables (% foliage cover of five vegetation layers: 2–4, 1–2, 0.5–1, 0.25–0.5, and 0–0.25 m). Point count data and plot density come from one and three study areas, respectively. Fitted lines are significant quadratic or linear relationships derived from LM for abundance and LMM for density. Numbers are R<sup>2</sup> of each significant relationship

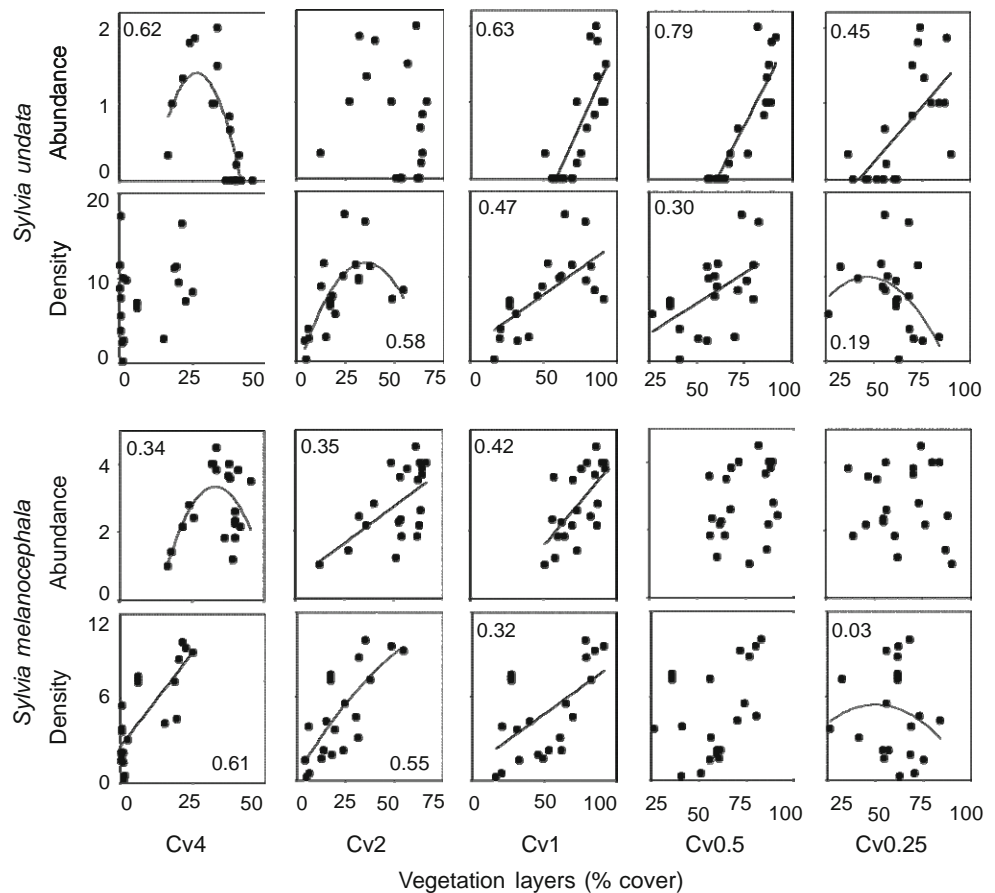
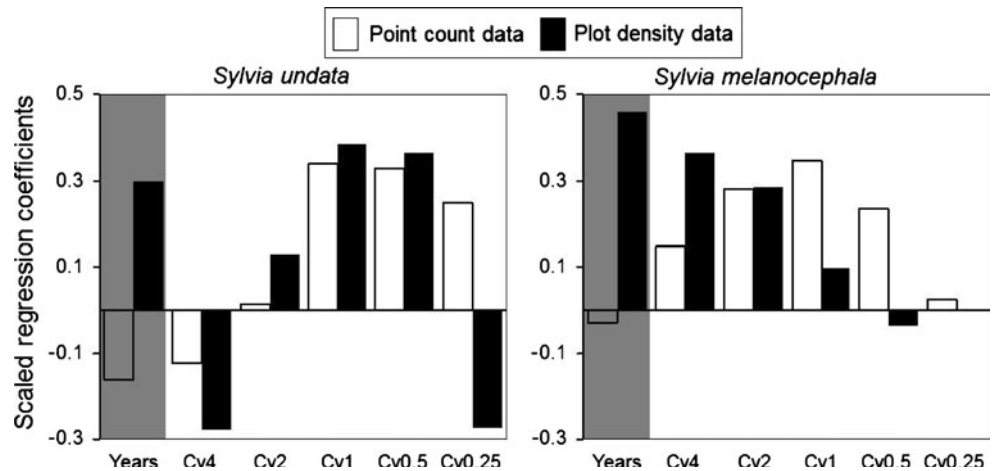


Table 2 Results of four partial least squares regressions (PLSR) analyses run for the two population measurements of Dartford (*Sylvia undata*) and Sardinian Warblers (*S. melanocephala*) (point count data and plot density coming from one and three study areas, respectively)

	Dartford Warbler						Sardinian Warbler					
	Point count data			Plot density			Point count data			Plot density		
	v1	v2	b	v1	v2	b	v1	v2	b	v1	v2	b
Log years since fire	-0.35	0.45	-0.16	0.20	0.50	0.30	0.39	-0.56	-0.03	0.24	0.84	0.46
Cv4	-0.30	0.55	-0.12	0.42	-0.80	<b>20.28</b>	0.47	-0.46	0.15	0.47	-0.01	0.36
Cv2	-0.17	0.61	0.01	0.55	-0.08	0.13	0.53	-0.26	0.28	0.55	-0.01	0.28
Cv1	0.41	0.50	0.34	0.57	0.05	0.39	0.49	0.43	0.35	0.54	-0.33	0.10
Cv0.5	0.54	0.33	0.33	0.47	-0.11	0.36	0.37	0.57	0.23	0.43	-0.57	-0.04
Cv0.25	0.57	-0.21	0.25	-0.03	-0.59	<b>20.27</b>	-0.10	0.66	0.02	0.00	-0.15	0.00
R <sup>2</sup> of Y	0.72	0.02		0.51	0.16		0.60	0.05		0.66	0.12	
R <sup>2</sup> of X	0.41	0.50		0.52	0.14		0.50	0.41		0.52	0.16	

The table shows the weights of the original variables for the two first latent vectors (v1 and v2) extracted by the each one of the PLSR analyses as well as the scaled regression coefficients (b). b-values larger than 0.20 (in absolute value) are highlighted in bold. Bottom rows show: (1) the proportion of the variance in the Y variable accounted for by the extracted vectors; (2) the proportion of the variance in the original X dataset (i.e. predictors) accounted for by the extracted vectors

Fig. 5 Scaled regression coefficients from partial least squares regressions (PLSR), showing the weights of the explanatory habitat variables on the point count data (coming from a single study area) and plot density (data from three study areas) of both warblers. Log-transformed year since fire and vegetation layers (foliage cover in %) at 2–4, 1–2, 0.5–1, 0.25–0.5, and 0–0.25 m are shown in abscissae



were mostly related to the low–intermediate layers between 25 cm and 1 m (Fig. 5), whereas time since fire showed contrasting coefficients (-0.16 and 0.30 for point count data and plot density, respectively; Table 2). In contrast to the pattern found for the Dartford Warbler, Sardinian Warblers were more strongly associated with intermediate and high vegetation layers (25 cm to 2 m based on point count data; 1–4 m based on plot density data). Plot density data showed a strong positive relationship with time since fire, although this was not evident in point count data (Fig. 5).

Finally, mean point count data and plot density in the LJ study area were highly correlated both in the Dartford ( $r = 0.888$ ,  $n = 8$ ; abundance log-transformed) and in the Sardinian Warbler ( $r = 0.838$ ,  $n = 8$ ; density log-transformed) for the first eight years after fire that could be tested.

Discussion

Our work synthesizes two datasets, one gathered by point counts over 22 consecutive years within the same forest area, and the other using three separate plots monitored for 4–8 years. This is one of the rare diachronic studies to record the complete population response, from colonization to local extinction, of a vertebrate species after disturbance. The response takes places in a particular time frame, i.e. the occurrence time-window, that depends on several factors, as we discuss below. The occurrence time-window of the Sardinian Warbler after fire could not be assessed as it was apparently longer than the duration of the study. This species, however, showed a peak of abundance 9 years after fire, after colonizing in the second year. The Dartford Warbler can colonize burned areas as soon as the second year after fire, even when it was absent before, as in LJ, and

provided that plant regeneration is vigorous. In the driest areas, as in TM, the species colonizes later, or remains confined to unburned patches. The peak of highest abundance may occur as soon as the fourth year after fire or later, up to the ninth year according to our data. The local extinction takes place 16 years or more following fire.

Our results also show the cover preferences of the two *Sylvia* warblers after fire, which, although similar overall, differ to some extent between the datasets. Sampling was more biased towards the early succession period in the plot dataset than in the point count dataset (median age after fire of 4 and 11.5 years, respectively). Plots, contrary to point counts, are distant from each other (the farthest, TO and TM, are separated by 62 km) and embrace different habitats: shrublands on limestone and siliceous substrates and forests. These differences help to explain why temporal patterns and vegetation layer preferences were not identical when comparing point count and plot density data.

In the LJ cork oak forest, the Sardinian but not the Dartford Warbler occurred before the wildfire, as shown by point counts. Thereafter, in the first year after fire, both warblers were absent. This study area was located within a severely burned landscape where foliage cover was very low in the first spring after fire, resulting mostly from sprouts of shrubs and cork oaks. The LJ plot was 1,700 m from the nearest unburned shrubland that could have acted as a colonization source (Brotons et al. 2005). In contrast, the TO, TM, and ER plots contained small unburned patches and were very close to unburned areas, which accounted for the persistence of a few breeding pairs of formerly present warblers. Afterwards, from the second year after fire, the Dartford Warbler sharply increased its density in two plots, LJ and TO, reaching  $\approx 8$  b.p./10 ha in response to a vigorous plant regeneration. In TO, specifically, top post-fire density of this species was reached in the sixth year after fire, being 75% higher than mean pre-fire density. In TM, a limestone garrigue, and in the coldest climate plot, ER (Table 1), pre-fire plot densities were smaller (5–7 b.p./10 ha) and post-fire recovery was much slower. On the other hand, the Sardinian Warbler had a slower and less marked population response (Fig. 3), in accordance with former studies (Herrando et al. 2001).

The Dartford Warbler disappeared from the cork oak forest point counts in the 16th year after fire and did not reappear from the 17th to 24th years after fire (R.P., personal observation), due to the development of the understory and canopy. In a 28-year study of a burned holm oak forest, the Dartford Warbler also colonized the area in the second spring after fire, was abundant up to the 6th year, appeared scarcely up to the 22nd year, and disappeared afterwards (Jacquet and Prodon 2009). In the same study, the Sardinian Warbler was one of the most common species from the 2nd to the 28th year. By contrast, at

1,400–2,100 m a.s.l. in the Pyrenees, the Dartford Warbler usually colonizes burned shrublands only after 5 years or more. Its abundance reaches a peak more than 20 years after fire and the bird is still occurring 50 years after fire (Pons and Clavero 2010). This delayed response was possibly due to the slow plant regeneration resulting from a colder climate and higher grazing pressure in the mountain area.

Cover preferences in the Dartford Warbler, derived from PLSR coefficients, were consistent between the point counts and the plots datasets. The only exception was the lowest layer (0–0.25 m), which is mostly herbaceous and highly variable among sites and years depending on soil and rainfall. The Dartford Warbler was more abundant when the cover between 0.25 and 1 m, its preferred layer for foraging and nesting (Bibby 1979; Glutz von Blotzheim and Bauer 1991; Martin and Thibault 1996; Shirihai et al. 2001), was dense. Layer preferences were not as consistent for the Sardinian Warbler, suggesting that environmental variables operating at larger scales, such as climatic conditions in winter (Herrando et al. 2001, Herrando et al. 2011), may affect population trends. This species showed, however, positive PLSR coefficients for the 0.5–4 m layers. The role of Mediterranean congeneric species in habitat preferences or in the occurrence of warbler species has not been assessed in this work. Recent studies have shown no competition effect of congenics on the Dartford Warbler and a possible effect of Rüppell's Warbler (*Sylvia rueppelli*), an Eastern Mediterranean species, on the Sardinian Warbler (Martin and Thibault 1996; Pons et al. 2008; Guillaumet and Prodon 2011).

Our results support the conclusion that the Dartford Warbler depends on the presence of dense and low shrublands. In most of the species' range, shrublands originate from wildfires in forests and former shrublands, and from land abandonment. In regions where succession toward forest is not hindered by climatic or edaphic limitation, such as the one studied here, shrublands depend on the disturbance regime (Blondel and Aronson 1999). Although logging and shrub clearing also contribute to shrubland formation and persistence, wildfires are the most important factor. In Catalonia, in the 1975–1998 period, 10.5% of wildland area burned once and 1.5% burned twice or more. The burned land included 23% of the existing shrubland area (Díaz-Delgado et al. 2004).

The high density of the Dartford Warbler in burned habitats, and its relatively short time-window of occurrence after fire, challenges the idea that wildfires are a threat for this bird in Mesomediterranean regions. Indeed, current forest encroachment, which tends to increase following fire suppression policies, represents a real threat (BirdLife International 2011). In vast areas of its breeding range, lack of management means that Dartford Warbler occurrence is



mostly dependent on fires. Its association with fire is not as strict as the one found in burned forest bird specialists like the Black-backed Woodpecker (*Picoides arcticus*) (Hutto 2008), but recalls the dependence on early successional habitats of Kirtland's Warbler (*Dendroica kirtlandii*) (Spaulding and Rothstein 2009). In Catalonia, for example, the Dartford Warbler's largest populations are found in frequently burned mountain areas (Pons 2004). On the other hand, in arid and soil-eroded regions of southeastern Spain and northern Africa, forest succession is often not possible and shrublands persist without fire. The uplisting of the Dartford Warbler as a globally near-threatened species should promote the study of its ecology in burned habitats and shed light on the threats and opportunities of fire-risk areas. Our work shows that the variations in the occurrence time-window of the Dartford Warbler after severe disturbance are mainly related to the speed of regeneration of the shrub layers. Precise knowledge on habitat regeneration could be used to predict the warbler's temporal occurrence at a local scale to anticipate habitat management when required for its conservation.

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