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OPEN-HABITAT BIRDS IN RECENTLY BURNED AREAS: THE ROLE OF THE FIRE EXTENT AND SPECIES' HABITAT BREADTH

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SUMMARY.—*Open-habitat birds in recently burned areas: the role of the fire extent and species' habitat breadth.*

Aims: To evaluate the occurrence of open-habitat and steppe-land bird species in Western Mediterranean burned areas and to assess the role of the extent and location of the fire on species richness and composition. At the species level, the relationship was explored between habitat breadth, distribution extent and the ability to occupy recently burned areas.

Location: Iberia and Southern France

Methods: Fieldwork and bibliography were assembled to obtain breeding bird inventories for 21 burned areas, mostly large wildfires (135- 23,800 ha). The sampling effort was standardized in relation to the area in the 11 fire locations surveyed using transects.

Results: Single burned areas contained 0 to 15 open-habitat species (mean = 7.6), and in all the areas combined there were 22 species, including 17 with an unfavourable conservation status in Europe. The most frequent were *Carduelis cannabina, Lullula arborea*, *Alectoris rufa*, *Oenanthe hispanica* and *Emberiza cia*, but characteristic steppe-land birds such as *O. leucura, Calandrella brachydactyla* and *C. rufescens* also bred in particular burned areas. After controlling for the extent of the species range in the Spanish distribution Atlas, passerine occurrence in burned areas was positively related to the species' habitat breadth in a gradient of unburned habitats. Cluster analysis separated a species-poor group of fire locations from a species-rich group, and showed that some neighbouring areas had a similar species composition. However, there was no spatial autocorrelation between burned areas, and species composition was correlated with the fire extent (Mantel test). Species richness tended to increase with increasing fire area. From the regression equation 5, 9, 12-13 and 16-17 open-habitat species may be expected to occur in burned areas of 100, 1000, 10,000 and 100,000 ha, respectively.

Conclusions: This study stresses the importance of biogeographical constraints on colonisation of new habitat patches created by disturbances. The extent of the fire rather than the proximity between burned areas influenced species richness and composition of open-habitat birds in recently burned areas. The best post-fire colonisers were generalists regarding habitat structure. The role of large wildfires in the conservation of threatened open-habitat birds seems to be significant and merits further study.

Key words: biogeography, colonisation, conservation, fire, passerines, species-area relationship, W Mediterranean.

RESUMEN.—*Aves de medios abiertos en áreas quemadas recientemente: la importancia de la extensión del fuego y la amplitud de hábitat de las especies.*

Objetivos: Evaluar la aparición de especies de aves de medios abiertos y esteparias en áreas quemadas del Mediterráneo occidental y valorar la importancia de la extensión y localidad del fuego en la riqueza y composición de especies. En el ámbito específico, exploramos la relación entre la amplitud de hábitat, el área de distribución y la habilidad para ocupar áreas quemadas recientemente.

Localidad: Península Ibérica y S de Francia

Métodos: Reunimos datos de trabajo de campo y bibliográficos para obtener inventarios de aves nidificantes de 21 áreas quemadas, mayoritariamente por grandes incendios (135- 23.800 ha). El esfuerzo de muestreo se estandarizó con relación al área para las 11 áreas prospectadas mediante transectos.

Resultados: Cada área quemada contuvo entre 0 y 15 especies de medios abiertos (media = 7,6) y en total aparecieron 22 especies, incluyendo 17 con categoría de conservación desfavorable en Europa. Las más frecuentes fueron *Carduelis cannabina, Lullula arborea*, *Alectoris rufa*, *Oenanthe hispanica* y *Emberiza cia*, aunque aves esteparias características, como *O. leucura, Calandrella brachydactyla* y *C. rufescens* también nidificaron en áreas concretas. Una vez controlada el área de distribución de las especies en el Atlas de aves nidificantes de España, la frecuencia de los paseriformes en las áreas quemadas se relacionó positivamente con

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la amplitud ecológica que éstas presentan sobre un amplio gradiente de hábitats no quemados. El análisis de conglomerados separó el grupo de localidades con pocas especies del grupo rico en ellas, y mostró que algunas áreas vecinas poseían una composición similar de especies. Sin embargo, no hubo autocorrelación espacial entre áreas quemadas y la composición de especies se correlacionó con la extensión del fuego (test de Mantel). La riqueza de especies también tendió a aumentar con el incremento del área quemada. Según se deduce de la ecuación de regresión, esperaríamos encontrar 5, 9, 12-13 y 16-17 especies de medios abiertos en fuegos de 100, 1000, 10.000 y 100.000 ha, respectivamente.

Conclusiones: Este estudio remarca la importancia de los factores biogeográficos en la colonización de los nuevos parches de hábitat credos por las perturbaciones. La extensión del fuego, más que la proximidad entre áreas, influyó en la riqueza y composición de especies de medios abiertos en áreas quemadas recientemente. Los mejores colonizadores post-fuego fueron generalistas respecto a la estructura del hábitat. El papel de los grandes incendios en la conservación de aves amenazadas de medios abiertos no parece insignificante y merece por ello una mayor atención.

Palabras clave: biogeografía, colonización, conservación, fuego, paseriformes, relaciones especies-área, Mediterráneo occidental.

INTRODUCTION

Open-habitat and steppe-land birds are among the most threatened birds in Europe, mostly due to widespread agricultural intensification across the continent (Tucker & Evans, 1997). Spain, that holds the main European populations of dry-land specialists, has experienced a high loss of cereal steppes in the plains resulting in species declines throughout the last fifty years (De Juana, 2004). In Mediterranean mountain ranges, traditional low-intensity farming could still be favourable for the biodiversity that depends on agricultural and grassland habitats. However, the long-term abandonment of marginal rough lands, together with modern afforestation practices, has led to a expansive increase in shrub and tree cover, especially in the northernmost Mediterranean basin (Debussche *et al*., 1999). As a result, many massifs are no longer suitable for open-habitat specialists, making local extinction already visible in Atlas studies (Martí & Del Moral, 2003). The process of landscape afforestation, together with climate warming and human activities, contributes to the increase in wildfire occurrence in the Mediterranean regions (Piñol *et al*., 1998). Fire reverses the afforestation process by temporarily modifying habitats. Recently burned areas can sometimes be colonised by open-habitat and steppe-land birds and this has led several authors to suggest the importance of fire in the conservation of threatened birds (Prodon, 1987; Vicente, 1991; Real, 2000).

Nevertheless, early occupancy of burned habitats by birds shows high spatial variability. Locally, it depends on the pre-fire bird community (Wooller & Calver, 1988; Pons & Prodon, 1996), the post-fire habitat structure (see, for example, Hobson & Schieck, 1999) and the site tenacity of the survivors (Pons *et al*., 2003a). On a larger scale, the magnitude and proximity of population sources has proved to be essential for colonisation by open-habitat species (Brotons *et al*., 2005). Other factors, such as the extent of the fire, its intensity and location and the regional landscape context may be important and should be studied using a biogeographical approach. The area is one of the main constraints on species richness (MacArthur & Wilson, 1967). The sampling effort, habitat diversity and colonization-extinction dynamics may explain why the number of species increases with increasing area. This relationship must also affect burned areas, independently of whether they act or not as ecological islands (Brotons *et al*., 2003). Despite its potential interest for the conservation of open-habitat birds, no data appear to exist on the species-area relationship in burned areas.

In this paper, an attempt is made to evaluate the occurrence of open-habitat and steppe-land bird species in a set of burned areas scattered throughout the Western Mediterranean. Analysis of several biogeographical constraints on bird colonisation, and specifically to assess the role of the extent and location of the fire on the species richness and composition, will be shown. On the species level, it is questioned whether there is a link between habitat breadth, distribution extent and the ability to occupy recently burned areas.

MATERIAL AND METHODS

Data sources

Data were gathered from 21 burned areas, mostly in Catalonia (NE Spain) but also scattered across N Portugal, NW Spain and S France (Fig. 1). All areas were located at similar latitude, between 40° and 44° N. Large burned areas were normally chosen to maximise the probability of colonisation by open-habitat birds. Most fires took place in summer, especially in August. Data were used both from personal fieldwork and bibliography but on the premise that a complete list of birds sampled at the start of the post-fire succession would be available. The presence or absence only of focal species was considered, and not their abundance at each location. Fire characteristics and specific data sources can be seen in Table 1.

1. Bibliographic studies

A total of 10 studies in SW Europe was selected, these focusing on wildfires larger than 100 ha (Pons & Prodon, 1996; Llimona *et al*., 2000; Herrando *et al*., 2003 and Guixé, *pers. obs*.), wildfires of unknown area (Martin, 1983; López & Guitián, 1988; Prodon, 1988; Almeida, 1991; Vicente, 1991) or a large amount of small prescribed burns (Moreira *et al*., 2003). Burned habitats were formerly pine or oak forests and scrublands. The studies sampled one to four breeding seasons in the five years after the fire. Due to the diversity of sampling designs used by the different authors, no attempt was made to correct differences in sampling methods, efforts or duration. For example, when trying to extract a single breeding season from all the studies three problems arose; (1) some studies provided pooled data for all the years, it was therefore impossible to separate a single year; (2) there was not a single common «age since fire» to all study areas; and (3) the annual sampling effort (in terms of time and monitored area) tended to be lower in those studies that lasted more than two years. The influence of the sampling on the results will be discussed later. It is considered that sampling was sufficiently intense in selected studies to closely estimate the real number of breeding species.

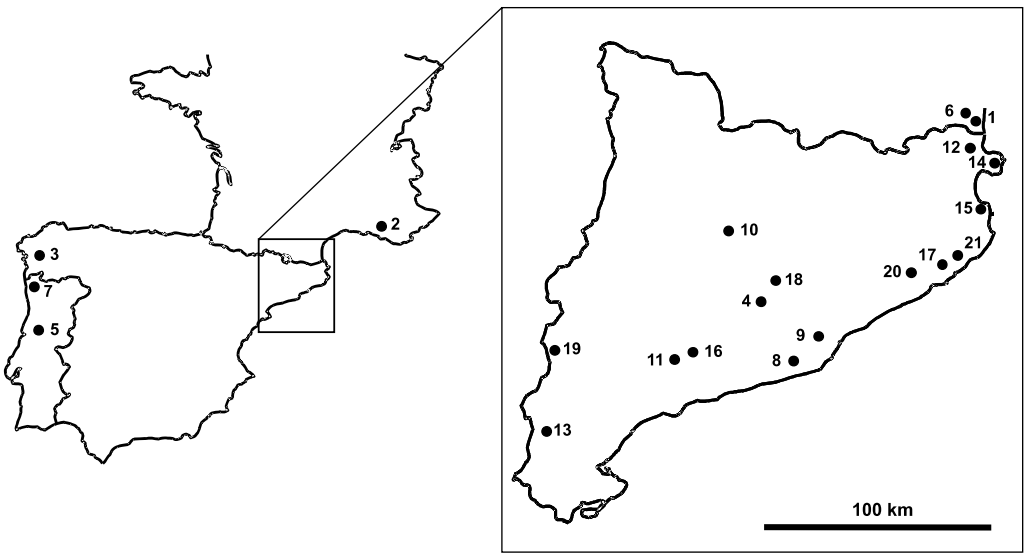

FIG. 1.—Location of the burned areas studied in Iberia and Southern France. The inset shows Catalan locations in detail. The location numbers correspond to Table 1.
[Localización de las áreas quemadas en la Península Ibérica y sur de Francia. El cuadro muestra el detalle de las localidades catalanas. La numeración de las localidades se corresponde con la de la Tabla 1.]

TABLE 1

Description of the fires used in this study, in chronological order. *Study year* refers to the age of the breeding seasons studied (1 = 1st breeding season since the fire, 2 = 2nd…), *Fire area* is measured in ha, *Reference* is abbreviated to the name of the first author followed by the publication year.
[Descripción de los fuegos usados en este estudio en orden cronológico. Año de estudio se refiere a la edad de la estación reproductora estudiada (1 = primera primavera desde el fuego, 2 = segunda…), Área quemada se expresa en ha. Las referencias se abrevian al nombren del primer autor seguido del año de publicación).]

Num.	Fire name *[Nombre]*	Main habitats *[Hábitat principal]*	Fire date *[Fecha]*	Study year *[Año de estudio]*	Fire area *[Área quemada]*	Reference *[Referencia]*
1	Pic Joan	Siliceous shrubland *[Matorral silíceo]*	Aug 78	1,2,3,4	Unknown	Prodon 88
2	Rove	Mixed habitats *[Hábitat mixto]*	≈ 1981	1	Unknown	Martin 83
3	Castro Valente	Maritime pine and shrubland *[Matorral y pinar resinero]*	≤ 1985	1,2,4	Unknown	López 88
4	Julenques	Calcareous shrubland *[Matorral calcáreo]*	Aug 86	3	Unknown	Vicente 91
5	Arganil	Robur-oak and chestnut *[Robledal y castañar]*	Sep 87	1	Unknown	Almeida 91
6	Mas Atxer	Siliceous shrubland *[Matorral silíceo]*	Aug 91	1,2,3	140	Pons 96
7	Minho	Maritime pine *[Pinar resinero]*	1992-97	1,3,5	Unknown	Moreira 03
8	Garraf	Aleppo pine and shrubland *[Pinar de carrasco y matorral]*	Jul 94	3	5000	Herrando 02
9	Collserola	Aleppo pine and holm-oak *[Pinar de carrasco y encina]*	Aug 94	1,2,3,4	135	Llimona 00
10	Solsonès	Austrian and Aleppo pines *[Pinos laricio y de carrasco]*	Jul 98	2,3	23800	Guixé unpubl.
11	l'Albiol	Aleppo pine *[Pinar de carrasco]*	Mar 00	2	634	present study
12	Garriguella	Shrubland and cork-oak *[Matorral y alcornocal]*	Aug 00	2	5905	present study

(Continúa)

TABLE 1 (Continuación)

Num.	Fire name *[Nombre]*	Main habitats *[Hábitat principal]*	Fire date *[Fecha]*	Study year *[Año de estudio]*	Fire area *[Área quemada]*	Reference *[Referencia]*
13	Prat de Comte	Aleppo pine and shrubland *[Pino de carrasco y matorral]*	Aug 00	2	273	present study
14	Cadaqués	Siliceous shrubland *[Matorral silíceo]*	Jun 01	1	1596	present study
15	l'Escala	Calcareous shrubland *[Matorral calcáreo]*	Jun 01	1,2	374	present study
16	Montblanc	Aleppo pine and shrubland *[Pino de carrasco y matorral]*	Aug 02	1	479	present study
17	Cristina d'Aro	Cork-oak *[Alcornocal]*	Jan 03	1,2	561	present study
18	Castellbell	Aleppo pine and shrubland *[Pino de carrasco y matorral]*	Jul 03	1	391	present study
19	Granja Escarp	Shrubland and Aleppo pine *[Pino de carrasco y matorral]*	Aug 03	1	2084	present study
20	Maçanet Selva	Mixed oak and pine *[Mixto de roble y pino]*	Aug 03	1	1257	present study
21	Castell d'Aro	Cork-oak and stone pine *[Alcornocal y pinar de piñonero]*	Aug 03	1	444	present study

2. Own transects

In Catalonia, 11 large wildfires were studied from 273 to 5905 ha, these having occurred in the two years prior to the bird censuses. All selected burned areas were located in mountain massifs with Mediterranean climatic conditions at low altitudes (100-500 m above sea level), their geographical centres were 8 to 280 km from one another. All the burned areas were formerly dominated by pine and oak forest, shrubland, mosaics containing open habitats and rocky outcrops to varying extents. For each burned area, bird censuses were conducted during the first or second breeding season (May-June, 2002 to 2004) after the fire. Within each fire perimeter a series of line transects (2-5) were established without limited census belts but restricted to birds positively occurring in the burned habitats. Transects were walked once during the morning by a single observer at a constant speed. They were located with the aim of recording all the focal species being studied with the condition that they had to traverse burned habitats. Unburned areas, agricultural habitats were not included in the censuses, and neither were fire edges if possible. For eight fires up to 1200 ha, the area surveyed by the

transects covered the burned area almost completely. For the three largest fires (>1500 ha) the transects were walked in a number of representative locations. Each transect was divided into 15-minute periods, making a total of 27 to 39 periods per burned area, depending on the extent of the fire. Within each of these periods, the occurrence (presence-absence) of any species either seen or heard was recorded.

Species selection

All species of open-habitat and steppe birds that occurred in the sampled burned areas were considered. Due to the lowland location of the areas studied, high altitude species were excluded. Open habitat and steppe species were defined as those generally occurring in drylands, rocky areas, grasslands, croplands, steppes and pseudosteppes in the Mediterranean region, and they were selected according to Prodon & Lebreton (1981), Estrada *et al*. (1996), Suárez *et al*. (1997), Tucker & Evans (1997), and Martí & Del Moral (2003). Ecotone and edge species such as most finches, and some shrikes and buntings were not included, and neither were shrubland specialists.

Data analysis

Cluster analysis was used to classify the locations according to their assemblages of open-habitat and steppe species. The square of the Euclidean distance was used as an association measure and complete linkage (also known as furthest neighbour sorting) as the agglomerative clustering method in order to increase the contrast between clusters (Legendre & Legendre, 1998). Mantel tests were used to test whether similarity in species occurrence was associated to distance between the study site locations. Subsequently, a partial Mantel test was performed to assess the relationship between species composition and fire extent, after taking into account the effect of the proximity between burned areas (Legendre & Legendre, 1998). The number of focal bird species was also related to the area logarithm using regression.

Passerines, excluding the Wheatear *Oenanthe oenanthe* that only occupies high mountains in most of the region, were then extracted from the original pool of species. Habitat breadth (HB) of passerines has been quantified in Spain (see Apéndice I in Martí & Del Moral, 2003), and defined as the distribution width of the focal species in the gradient of vegetation structure. The HB is calculated from the mean of the species' three maximum densities in six unburned habitat classes (Carrascal & Lobo, 2003). The number of burned areas in which the species occurred was related to its HB by a partial correlation, taking into account the distribution extent of each species in Spain (Martí & Del Moral, 2003). This approach was used to correct the predictably positive link between the range of the species and its occurrence in separate wildfires.

RESULTS

A total of 22 open-habitat species, 19 passerines and 3 non-passerines occurred shortly after the fire in the 21 burned areas in Iberia and Southern France. The frequency distribution of species in burned areas can be seen in Figure 2a and the detailed dataset in Appendix 1. Single areas contained 0 to 15 open-habitat species (mean = 7.6, Fig. 2b). The most frequent (occurring in more than 10 locations) were the Linnet *Carduelis cannabina*, Woodlark *Lullula arborea*, Red-legged Partridge *Alectoris rufa*, Black-eared Wheatear *Oenanthe hispanica*, Rock Bunting *Emberiza cia*, Stonechat *Saxicola torquata* and Corn Bunting *Miliaria calandra*. On the other hand, characteristic steppe-land birds such as Short-toed Lark *Calandrella brachydactyla*, Lesser Short-toed Lark *C. rufescens* and Black Wheatear *Oenanthe leucura* only bred in one or two burned areas. In contrast, several open-habitat and steppe-land species were not present at all, such as the Pin-tailed Sandgrouse *Pterocles alchata,* Black-bellied Sandgrouse *Pterocles orientalis,* Montagu's Harrier *Circus pygargus,* Roller *Coracias garrulus*, Calandra Lark *Melanocorypha calandra,* Fan-tailed Warbler *Cisticola juncidis* and Spectacled Warbler *Sylvia conspicillata*, although the latter has been sometimes found after recent fires (Prodon, 1988). Similarly, the Tree Pipit *Anthus trivialis,* Red-backed Shrike *Lanius collurio* and Yellowhammer *Emberiza citrinella* that occur in recently burned areas in the highlands of the region (Pons *et al*., 2003b)

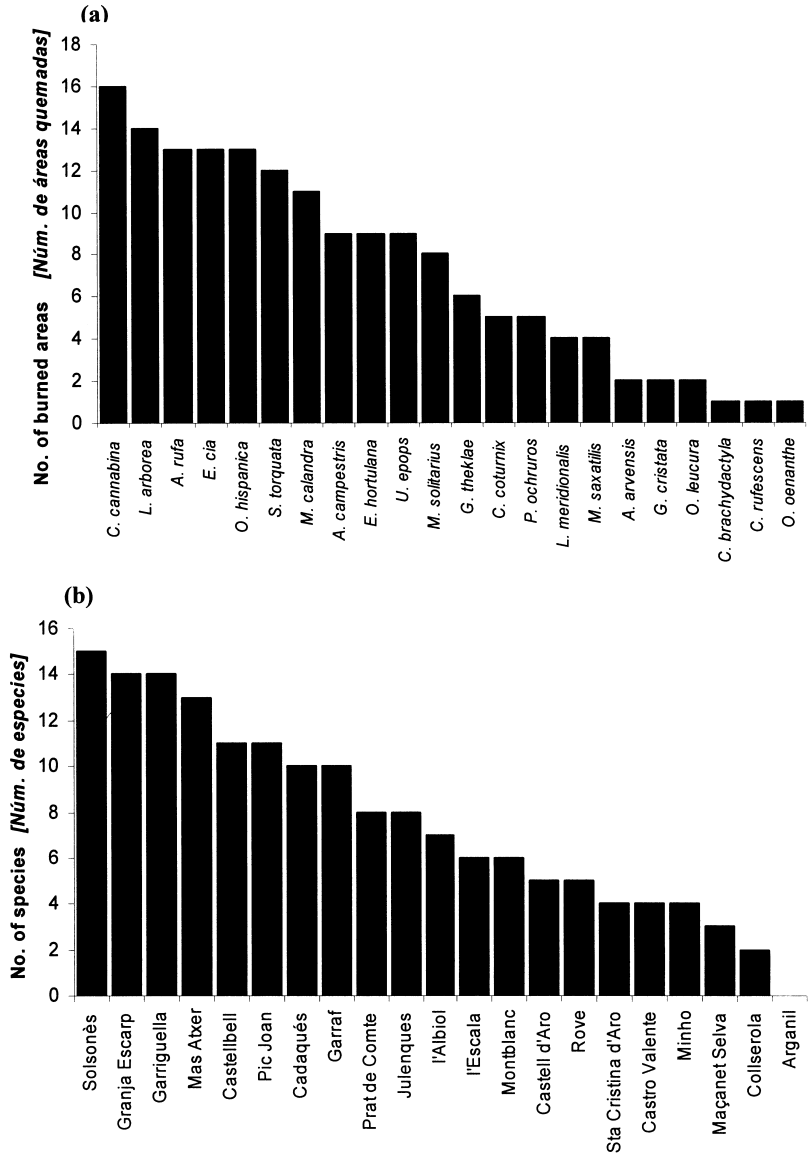

FIG. 2.—Frequency distribution for the 22 open-habitat bird species in the 21 burned areas (a) and species richness per location (b).
[Distribución de frecuencias de las 22 especies de aves de medios abiertos en las 21 áreas quemadas (a) y riqueza de especies por localidad (b).]

were also absent from the locations studied. Seventeen out of the 22 observed species (77% of the total) have an unfavourable conservation status in Europe (SPECs 2 and 3 in Tucker & Heath, 1994). Most remarkably, the four SPEC-2 species occurred in 43% to 67% of the locations (the Red-legged Partridge in 13 locations, the Woodlark in 14, the Black-eared Wheatear in 13 and the Ortolan Bunting *Emberiza hortulana* in 9).

Cluster analysis of the 20 burned areas (one study site in Portugal with none of the focal species in it was excluded) firstly separated into two main groups (Fig. 3). The upper group contains species-poor locations (2-7 species) and the lower group contains species-rich locations (8-15 species) with the exception of one location (Rove, with only 5 species). Subsequently, the main groups are divided into smaller sets, some only including neighbouring burned areas but others including areas separated by more than 900 km. Two particular burned areas in inland Catalonia are also separated trunkally because they contain exclusive or infrequent species; the Skylark *Alauda arvensis*, Crested Lark *Galerida cristata* and Wheatear in Solsonès and the Short-toed larks and Black Wheatear in Granja d'Escarp. The similarity between the species occurrence patterns for 18 burned areas, once the two extremely distant locations in Galicia and Portugal were excluded, did not decrease with the increasing geographical distance (Mantel test, Spearman r = 0.135, one-tailed P = 0.103). In the 15 locations for which the area was known (all of them in Catalonia) there was a significant correlation between species composition and fire extent, once the effect of the distance between locations was taken into account (partial Mantel test, Spearman r = 0.490, one-tailed P = 0.001).

The predictable species-area relationship complies with the dataset for 15 locations of known area (Fig. 4). According to the regression equation (N species = 3.837 logArea - 2.778, r = 0.569, P = 0.027) it may be expected of finding about 5 open-habitat species after a fire of 100 ha, around 9 species after a 1,000-ha fire, 12-13 species after a 10,000-ha fire and 16-17 species after a 100,000-ha fire. The number of burned areas in which a particular species occur was correlated both to its HB and to its distribution extent in Spain (r = 0.710, one-tailed P < 0.001 and r = 0.538, one-tailed P = 0.011, respectively; n = 18). Once controlled for the range of the species in the Spanish distribution Atlas, it can be seen that the most commonly occurring passerines in burned areas tend to have the highest habitat breadth in the vegetation gradient (r = 0.577, one-tailed P = 0.008, df = 15). The relationship between habitat breadth and frequency of occurrence in fire locations is shown in Figure 5.

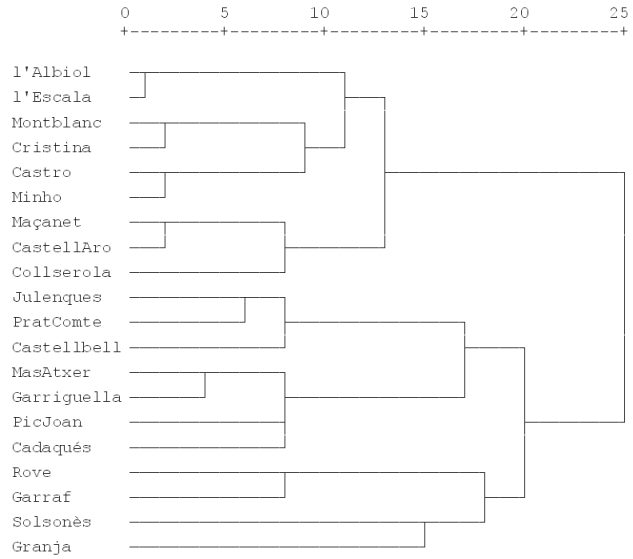

FIG. 3.—Cluster diagram of the W Mediterranean burned areas studied, based on the complete linkage method and the Euclidean distance computed using the species composition of the locations.
[Diagrama de conglomerados de las áreas quemadas estudiadas en el Mediterráneo Occidental, basado en el método de vinculación completa y en la distancia Euclidea calculada utilizando la composición de especies de las localidades.]

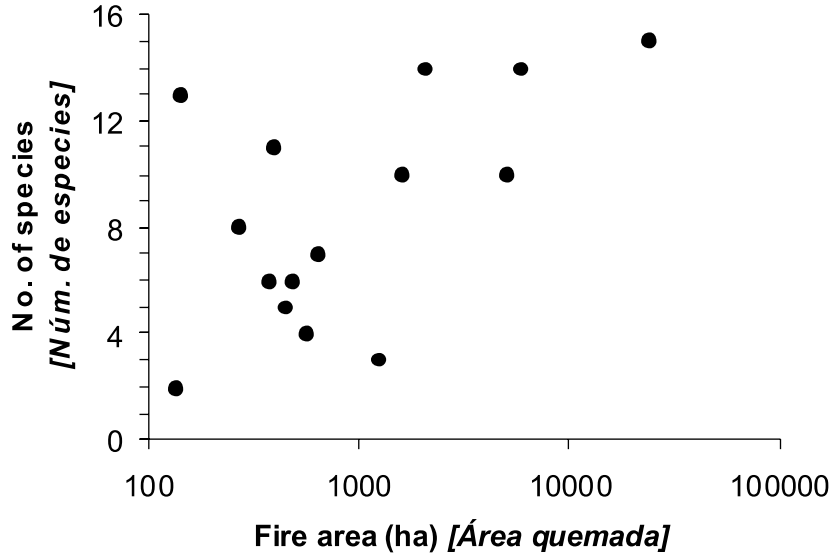

FIG. 4.—Species-area relationship for the 15 fires of known area (area in logarithm).
[Relación especies-área para los 15 fuegos de área conocida (área en logaritmo).]

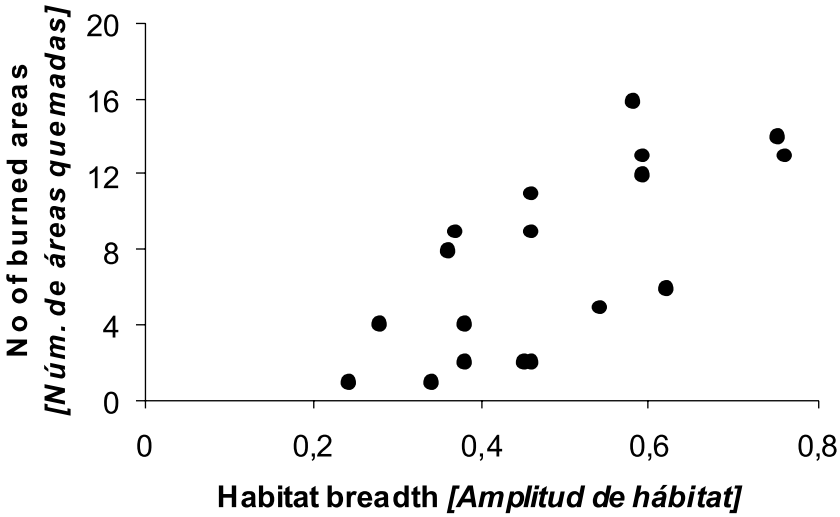

FIG. 5.—Species frequency of occurrence in burned areas as a function of habitat breadth for the 18 open-habitat passerine species. Habitat breadth data from Carrascal & Lobo (2003), calculated from a gradient of multiple unburned habitats in Spain.
[Frecuencias específicas de aparición en las áreas quemadas en función de la amplitud de hábitat para las 18 especies de paseriformes de medios abiertos. Los datos de amplitud de hábitat se han tomado de Carrascal & Lobo (2003), calculados en base a un gradiente de múltiples hábitats no quemados en España.]

DISCUSSION

The results of this study stress that the extent of the fire is more important than proximity between burned areas when explaining open-habitat species richness and composition. The lack of a significant species spatial autocorrelation was mainly due to low similarity between several species-rich burned areas and nearby species-poor burned areas. Concerning the species-area relationship, it could be argued that it is simply a consequence of an increase in sampling effort. The sampling effort is controlled for in our own fieldwork with the aim of standardizing the survey efficiency in relation to the area (Abbott, 1983). It was impossible to do so for the bibliographic dataset. However, only four fires of known size from the literature entered into the species-area model, and in these locations a more local sampling was compensated for by a longer study. Overall, it is thought that the species number was correctly estimated for fire locations with different areas because sampling was intense enough to closely approximate the real number of breeding species. It is therefore suggested that the species-area relationship observed arises for two main reasons. First, more immigrants colonise large burned areas because of the higher probability of discovering the newly burned patch and finding a suitable habitat there. Despite area being considered as relatively unimportant in determining immigration to islands (Wiens, 1989), the probability of a bird detecting a 100-ha or a 20,000-ha burned patch is obviously different. More importantly, the trend for an increase in habitat diversity with increasing area allows more species to breed in larger burned areas. Secondly, it is more likely that large areas contain pre-fire populations of open-habitat species linked to rocky, grassy or bare ground areas (Pons & Prodon, 1996). Individuals, during juvenile dispersal for example, could simply spread to neighbouring unvegetated land after the fire.

It is also certain that factors not linked to area, such as the regional landscape context, greatly affect the number and identity of species. Burned areas in the centre of large wooded areas (as is the case of Cristina d'Aro in the Cadiretes massif) or areas next to intensive agricultural or urbanised areas (Collserola in the Metropolitan region of Barcelona) behave as islands for most open-habitat species that will likely not colonise from distant sources (Brotons *et al.*, 2005). On the other hand, burned areas next to low-intensity farming (such as the Mas Atxer fire in the vineyard region of the Albera chain) may be species-rich despite the burned area being small. When an agroforested mosaic landscape is combined with a large affected area the species number is highest (Solsonès, Granja d'Escarp and Garriguella are the main examples). Solsonès had two exclusive cropland species because of its fine-grain mosaic of pine forests and cereal crops, whereas Granja d'Escarp had two exclusive steppe-land species because it is the only pseudosteppe location. The area and type of forest, whether it has been cut or not and to what extent, are other essential features after a fire. All the study areas contained wooded and unwooded habitats and many had been subjected to some logging after the fire. This is reflected to some extent in the species composition because more open-habitat species are able to colonise burned scrubland or logged forest than can colonise an unlogged forest. The Woodlark, for instance, needs some trees remaining to install its territory but dense standing trees constitute a serious barrier for it. Moreover, post-fire tree regeneration is highly variable: no or very low regeneration of the Austrian pine *Pinus nigra*, extensive germination of the Aleppo pine *Pinus halepensis*, trunk sprouting in most oaks *Quercus spp.,* and branch sprouting in the cork-oak *Quercus suber*. The regeneration of grass and scrub cover is also very different within and between burned areas. It seems that the Quail *Coturnix coturnix* and the Corn Bunting, among others, need developed grass cover in order to colonise burned areas. In contrast, the lignification of regenerating shrubs, mainly from the third year after the fire, makes foraging difficult for most open-habitat and steppeland species (Prodon, 1988).

A broad species' habitat breadth is also fundamental to allow colonisation of recently burned areas. Specialized birds such as several steppe-land, rocky or farmland species are very rare at the surveyed locations. It has been shown that this trend is mostly unrelated to the size of the species' range in the region. It is more likely that the resources available in the disturbed ecosystem do not match their specific requirements. The causes of absence, however,

can diverge. Sandgrouses, Montagu's Harrier, Roller and Spectacled Warbler that never occured in the 22 burned areas have a tiny population at the regional scale (Galicia, N Portugal, Catalonia and S France), whereas Calandra Lark and Fan-tailed Warbler were common in the surroundings of several burned areas but did never sing on them, possibly because of topography and vegetation structure. On the other hand, it is striking that more than 20 open-habitat species use recent fires. It demonstrates a widespread phenotypic plasticity allowing them to cope with transformed habitats. Essential behaviour such as foraging, nest site selection, anti-predator responses, roosting, etc. must be modified and adapted to the new habitat structure and resources. It is, however, not well known whether the demography of such pioneer species is negatively affected in burned areas (but see Saab & Vierling, 2001; Pons *et al*., 2003a).

The effects of repeated wildfires on Mediterranean vegetation are now beginning to be assessed on a regional scale (Díaz-Delgado *et al*., 2002; Lloret *et al*., 2002). Fire is shaping landscapes in large areas, especially where management is scarce and vegetation evolves towards continuous young forests, which is common in a wet Mediterranean climate. In this context, the need for a large-scale approach to the distribution and conservation of animals is essential. The pioneer studies of Moreira *et al*. (2001) and Herrando & Brotons (2002) stress the role of a fire regime in maintaining bird diversity at the landscape level. Despite large fires usually being perceived as being the most destructive, the opposite is true for our set of species, which grew from 5 to 12-13 species when the burned area increased from 100 to 10000 ha. Taking into account the effects of area and isolation on metapopulation dynamics, and the temporary character of most open habitats created by farming, logging or fire, a heterogeneous landscape seems to be essential for open-habitat birds in the Mediterranean. A regional approach to landscape management is thus required in heavily wooded regions if the conservation of threatened species and the avoidance of very large wildfires are targeted .

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APPENDIX 1 *[Ápéndice 1]*

Open-habitat bird species occurrence in 20 burned areas (location number 5 had no species and has therefore been excluded). Categories of the Species of European Conservation Concern (SPECs) correspond to Tucker & Heath (1994), SPEC 2 and 3 mean an unfavourable conservation status in Europe. See Table 1 for the fire description and Figure 1 for fire location. F = frequency of species occurrence in burned areas.
[Aparición de las especies de aves de medios abiertos en 20 áreas quemadas (la localidad número 5 no presentó ninguna de estas especies y ha sido por ello excluida). Las categorías de las Species of European Conservation Concern (SPECs) *se han tomado de Tucker & Heath (1994), SPEC 2 y 3 equivale a un estatus de conservación desfavorable en Europa. Véase la Tabla 1 para una descripción de los fuegos y la Figura 1 para su localización. F = Frecuencias específicas de aparición en las áreas quemadas]*

SPEC	Fire number *[Número del fuego]*	1	2	3	4	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	F
3	*Alauda arvensis*	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
2	*Alectoris rufa*	1	1	0	0	1	0	1	0	1	1	1	0	1	1	0	0	1	1	1	1	13
3	*Anthus campestris*	0	1	0	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	9
3	*Calandrella brachydactyla*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
3	*Calandrella rufescens*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
4	*Carduelis cannabina*	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	16
3	*Coturnix coturnix*	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	1	5
3	*Emberiza cia*	1	0	1	1	1	1	1	0	1	1	1	1	0	0	1	0	1	1	0	0	13
2	*Emberiza hortulana*	1	1	0	1	1	0	1	0	1	0	1	0	1	0	0	0	1	0	0	0	9
3	*Galerida cristata*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2
3	*Galerida theklae*	1	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	6
3	*Lanius meridionalis*	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	4
2	*Lullula arborea*	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	14
4	*Miliaria calandra*	1	0	0	1	1	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	11
3	*Monticola saxatilis*	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	4
3	*Monticola solitarius*	1	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	8
2	*Oenanthe hispanica*	1	1	0	1	1	0	1	0	1	0	1	1	1	0	1	1	1	1	0	0	13
3	*Oenanthe leucura*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
—	*Oenanthe oenanthe*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
—	*Phoenicurus ochruros*	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	5
3	*Saxicola torquata*	1	0	1	0	1	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	12
—	*Upupa epops*	0	0	0	1	0	0	0	1	1	1	1	1	0	1	0	0	1	1	0	0	9
	n of species	11	5	4	8	13	4	10	2	15	7	14	8	10	6	6	4	11	14	3	5	