CONNECTIVITY DETERMINES POST-FIRE COLONISATION BY OPEN-HABITAT BIRD SPECIES: THE CASE OF THE ORTOLAN BUNTING *EMBERIZA HORTULANA*

LA CONECTIVIDAD DETERMINA LA COLONIZACIÓN POST-INCENDIO POR AVES DE HÁBITATS ABIERTOS: EL CASO DEL ESCRIBANO HORTELANO *EMBERIZA HORTULANA*

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Summary.—Wildfires are certainly a key natural disturbance to terrestrial Mediterranean ecosystems. After an intense fire different types of habitats revert to relatively similar open hábitats. This early successional stage has been shown to be used by many open-habitat bird species, which are able to colonise these new suitable habitats. By adopting a regional scale perspective, we assessed to what extent post-fire colonisation by open-habitat birds is constrained by the degree of isolation of burnt areas or the size of the burnt patch, and analysed the influence of the period elapsed since a fire on species colonisation. We focused on the Catalan population of the ortolan bunting *Emberiza hortulana* and estimated the amount of dispersal flux into a number of recently burnt areas as a measure of patch isolation, using regional data derived from atlas surveys and connectivity metrics based on graph theory. Our results show that species occurrence on recently burnt areas was primarily driven by the amount of dispersal flux, and to a lesser extent by the extent of the burnt area. Species occurrence also tended to increase with time since fire, suggesting that effective colonisation was partly driven by stochastic ecological and behavioural processes. We suggest that the prediction of species' responses

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to disturbances on large spatial scales should explicitly integrate not only species' responses to habitat changes but also information on dispersal constraints imposed by species' ecology.

Key words: ecological networks, graph theory, landscape context, metapopulation theory, population sources.

RESUMEN.—Los incendios son una perturbación natural en los ecosistemas Mediterráneos terrestres. Como consecuencia del paso del fuego, diferentes tipos de hábitats se transforman en hábitat abiertos similares entre si. Muchas especies de aves que ocupan hábitats abiertos colonizan el nuevo hábitat creado después de los incendios durante los primeros años tras la perturbación. En este trabajo se analiza hasta qué punto la colonización de las aves de hábitats abiertos está limitada por el grado de aislamiento de las zonas quemadas o por el tamaño de las zonas quemadas, y se investiga también el efecto del tiempo transcurrido después del fuego en el proceso de colonización. El estudio se centra en la población de Cataluña del escribano hortelano *Emberiza hortulana* y se estima la cantidad de flujo de dispersión recibida en un conjunto de zonas recientemente quemadas como una medida de la conectividad del paisaje utilizando información regional derivada del Atlas e índices de conectividad basados en la teoría de grafos. Nuestros resultados demuestran que la presencia de la especie en zonas recientemente quemadas está principalmente limitada por la cantidad de flujo de dispersión y en menor medida por el tamaño del incendio. Además, la probabilidad de colonización se incrementó con el número de años transcurridos después del incendio, sugiriendo que el proceso de colonización está condicionado por procesos estocásticos. Se concluye que la predicción de la respuesta de las especies a las perturbaciones a grandes escalas espaciales debería incluir no sólo la respuesta de las especies a los cambios en el paisaje sino también información sobre la dispersión de las especies.

*Palabras clav*e: contexto paisajístico, fuentes poblacionales, redes ecológicas, teoría de grafos, teoría de metapoblaciones.

INTRODUCTION

The persistence of species at the metapopulation level depends on a stochastic equilibrium between local extinctions and colonisations of suitable habitat patches. Both processes are considered as the key components of metapopulation theory (Hanski, 1999), which relies heavily on patch size and isolation in order to explain species' spatial dynamics (e.g., Hanski, 1994; Moilanen and Hanski, 1998). Small populations are believed to be more prone to extinction than large ones, while the colonisation probability of an empty patch is largely determined by its isolation from surrounding populations. Traditionally, these studies have focused on these processes using models that simplified assumptions concerning the long-term persistence of patches and the time-scale separation between local

and global dynamics. However, most habitats are affected, at least to some degree, by dynamics related to disturbances and their subsequent successional processes (Biedermann, 2005; Vuilleumier *et al*., 2007).

The nature of patchiness induced by a disturbance affects the level of resource availability in the disturbed patches, the species' survival in the patch and the rate of colonisation and success of establishment of new species (Sousa, 1984; Pickett and White, 1985). Wildfires represent an important natural disturbance to Mediterranean terrestrial ecosystems (Trabaud, 1994; Whelan, 1995), shaping landscapes into their present mosaic-like patterns (Piussi, 1992; Naveh, 1994). After an intense fire, habitats with different vegetation cover and structure converge towards becoming structurally simpler open habitats that will progressively tend to more

complex vegetation structure in time (Trabaud and Lepart, 1980; Lloret *et al.*, 1999). This early successional stage has been shown to be used by many open-habitat bird species (Herrando *et al.*, 2002; Pons and Bas, 2005; Castro *et al.*, 2010), which are able to colonise these new suitable habitats. Several studies have focused on factors affecting bird community responses to fire (Pons and Prodon, 1996; Moreira *et al.*, 2001; Herrando *et al.*, 2002; Jacquet and Prodon, 2009) but there is rather limited knowledge on the factors determining species' capacity to colonise burnt areas. Recent studies have suggested a strong role of dispersal on post-fire bird species' colonisation (Brotons *et al.*, 2005, 2008).

This work focused on a Mediterranean population of ortolan buntings *Emberiza hortulana*, an open-habitat bird species linked to recently burnt areas (Dale and Olsen, 2002; Revaz *et al.*, 2005; Pons and Bas, 2005). This species has suffered large-scale declines across Europe during the last few decades (BirdLife International, 2004). This decrease appears to be related to general habitat loss and degradation as a consequence of homogenisation of agricultural landscapes and farming intensification (Dale, 2001; Vepsalainen *et al.*, 2005). Nevertheless, in Catalonia (north-eastern Spain) the ortolan bunting has almost doubled its breeding range in the last 20 years (Estrada *et al.*, 2004). Whereas the main trends in agricultural practice there appear to be similar to those prevailing in other European regions (Sirami *et al.*, 2007), in Catalonia wildfires have recently been suggested as a potential cause of the expansion of the species, by creating suitable habitats for the colonisation and persistence of their populations (Brotons *et al.*, 2008).

The objective of the present study was to assess to what extent the colonisation of recently burnt areas by the ortolan bunting is constrained by the degree of isolation of burnt sites or by the extent of the fire. We es-

timated the amount of dispersal flux received in a set of burnt areas occurring in the region as a measure of patch isolation, using regional data derived from atlas surveys and connectivity metrics based on graph theory, and evaluated our predictions using bird data specifically gathered for this purpose. Using the metapopulation framework as a baseline, we hypothesised that colonisation of newly created patches is more related to patch connectivity than to habitat availability in the newly burnt areas. Finally, if stochastic processes such as the probability of finding a new habitat patch or finding a mate constrain effective species colonisation of recently burnt areas, we expect that the length of the period elapsed since the fire will play an additional role in explaining species' occurrence patterns in burnt areas.

MATERIAL AND METHODS

Study region and site selection

The study was carried out in Catalonia, a region dominated by Mediterranean climate and located in the north-eastern corner of Spain. Our first aim was to identify wildfires that had affected an area of more than 50 ha of forest and/or shrubland between 2000 and 2006, resulting in the location of 49 sites (fig.1 and Appendix 1). Fire perimeters were provided by the *Departament de medi ambient i habitatge* (DMAH) of the Catalan government.

The selected wildfires had affected areas ranging from 51 to 4,491 ha (fig. 2) and were all located in mountain massifs with similar Mediterranean climatic conditions, at low-mid altitudes (100-1,300 m above sea level). All sites were formerly dominated by forest (mainly pine: *Pinus halepensis*, *P. sylvestris* and *P. nigra*, cork oak *Quercus suber* or holm oak *Quercus ilex*) and shrubland mosaics comprising open habitats; such as clearings,
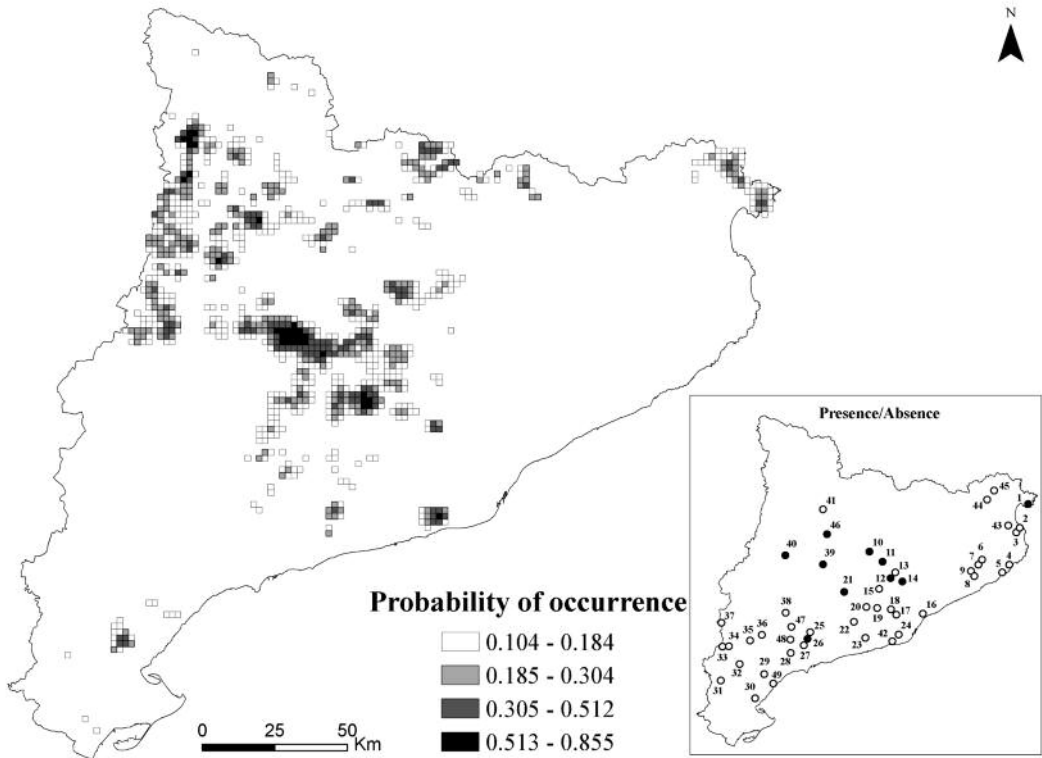
FIG. 1.—Probability of occurrence of the ortolan bunting in 2 × 2 km squares in Catalonia. The map on the lower right corner shows ortolan bunting presence (in black) and absence (in white) in the studied wildfires. Numbers correspond to wildfire codes (see Appendix 1).
[Probabilidad de presencia del escribano hortelano en cuadrículas UTM 2 × 2 km en Cataluña. El mapa de la esquina inferior derecha muestra la presencia (en negro) y la ausencia (en blanco) del escribano en las zonas incendiadas registradas en este estudio. Los números corresponden a los códigos de los incendios (véase Apéndice 1).]

old fields and dry grasslands, and rocky outcrops of variable extent. Fires took place in late winter (late January-early March) or in summer (June-August), and affected the forest canopy and undergrowth, causing widespread tree mortality (Rodrigo *et al.*, 2004).

Post-fire bird sampling

We used bird data from a monitoring program described by Zozaya *et al.* (2010) investigating bird species' responses to recent wildfires in Catalonia. The project started in 2006 and monitors all wildfires from 2000 in which more than 50 ha of forest and/or shrubland were affected. Within each fire perimeter a number of line transects of 15 minute duration are followed. In this way, an observer travels along a transect and notes the presence and abundance of all species, and allocates them into one of the four distance bands (0-25 m, 25-50 m, 50-100 m, >100 m). Surveys are conducted once every breeding
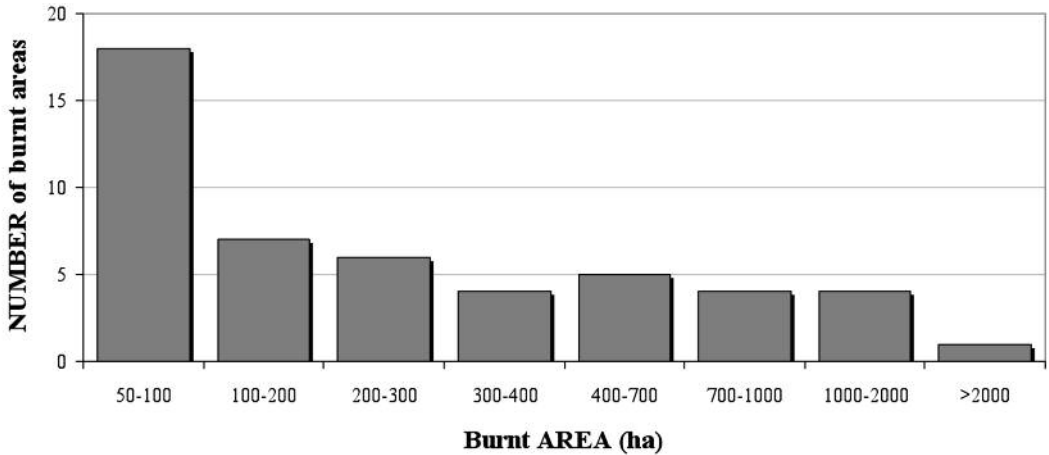
FIG. 2.—Fire size distribution.
[Distribución del tamaño de las superficies incendiadas.]

season (10th May-15th June) in good weather conditions (i.e. without rainfall or strong wind) during the first three hours after sunrise by experienced ornithologists, moving at a speed of about 2 km/h (Zozaya *et al.*, 2010).

The number of transects per fire was calculated following a linear function of the logarithm of fire area. The establishment of transects within the burnt areas observes the following criteria: a) they are conducted entirely across burnt land avoiding unburnt patches (forest or farmland) and fire edges where possible; b) the minimum distance between two transects is 150 m; c) the minimum distance between transects and fire edge is 50 m; d) transects are conducted preferably on existing trails in order to allow future repetition of the transects after vegetation recovery and, e) in the largest burnt areas, transects are distributed in a number of representative locations covering habitat heterogeneity within the fire perimeter. The number of transects conducted in each of the burnt areas studied is given in Appendix 1.

The present study used bird surveys conducted in two consecutive years (2006 and 2007) in areas that had been burnt between 2000 and 2005, as well as during the first three years after each fire event for fires that occurred in 2005 and 2006. The occurrence (presence or absence) of the ortolan bunting within 100 m-wide strips on both sides of every track was noted.

Amount of dispersal flux received in each of the studied burnt sites

We used a graph theory-based approach to estimate the amount of dispersal flux received in each of the studied burnt locations as related to a measure of patch connectivity. According to this theory, a landscape ('graph' in graph theory literature) is conceived as a set of habitat patches (nodes) and connecting elements ('links'). In this sense, a landscape element, *i,* that contains habitat area is considered a habitat patch (Urban and Keitt, 2001) and is here characterized by an attribute value (a_i). On the other hand, a link is defined as an element that comprises no habitat area and represents the potential of

an organism to disperse directly between two habitat patches through favourable land cover. Links are here considered symmetric, i.e. the probability of dispersal from patch i to patch j is the same as that from patch j to patch i.

In this work we differentiated two types of nodes: (1) the nodes corresponding to the habitat patches explaining ortolan bunting distribution, before the impact of selected wildfires (n = 945) and (2) the nodes corresponding to the new suitable habitat patches that appeared after the studied fires (n = 49). We used available regional data on species distribution derived from the *Catalan Breeding Bird Atlas 1999-2002* (Estrada *et al.*, 2004) to identify the potential sources of colonisers. The Atlas provides the probability of occurrence of the ortolan bunting in 1×1 km squares covering all Catalonia, as a result of field sampling and niche-based modelling (Estrada *et al.*, 2004). Atlas data were collected before any of the wildfires studied here occurred, which allowed their use for further analyses. Based on this data source, the distribution of the ortolan bunting is concentrated in central and northwestern Catalonia, in a number of scrubby massifs near the coast and locally in the Pyrenees up to 2,400 m (Pons, 2004). For this study, we calculated the probability of species occurrence in each of the 2×2 km squares (as the mean value of the four adjacent 1×1 km squares) and selected as sources of colonisers those squares with a value greater than 0.1 (the smallest probability of species occurrence where it was found during field work). This gave a total of 945 nodes (2×2 km squares) characterised by the probability of species occurrence (fig. 1). We used a spatial resolution of 2×2 km squares in order to allow efficient processing with some of the indices implemented in the Conefor Sensinode software (see below), which may become unfeasible for graph structures with large number of nodes. Furthermore, in order to

characterise the links, we used centroid-to-centroid Euclidean distances between nodes and a median breeding dispersal distance of 12 km, close to that observed in an ortolan bunting population in Norway (Dale *et al.*, 2005, 2006).

Once we established the matrices of nodes and distances we estimated the amount of dispersal flux received in each of the selected burnt sites by using two connectivity metrics: the integral index of connectivity (IIC) (Pascual-Hortal and Saura, 2006) and the probability of connectivity (PC) (Saura and Pascual-Hortal, 2007), both implemented in Conefor Sensinode software (CS) (Saura and Torné, 2009, http://www.conefor.org). The two metrics differ from one another in that IIC is based on a binary connection model (habitat patches are either connected or not connected) while PC relies on a probabilistic connection model (there is a certain probability of direct dispersal between patches i and j, p_{ij}). In this sense, IIC assigned a link between two habitat patches if the distance between them was smaller than or equal to 12 km. Whereas for PC a probability of direct dispersal $p_{ij} = 0.5$ was set for a distance of 12 km and a negative exponential function was used to obtain the p_{ij} between every two habitat patches as a function of the distance between them (e.g. Urban and Keitt, 2001; Saura and Pascual-Hortal, 2007). Using IIC, the amount of dispersal flux is calculated as:

$$Flux_{k, IIC} = \sum_{i \neq j}^{n} \frac{a_i \cdot a_j}{1 + nl_{ij}} \qquad (1)$$

where a_i is the attribute of the new habitat patch appearing in the landscape as a consequence of a fire (k). In this study, the attribute value of the nodes corresponding to the burnt sites was considered as 1 to ensure independence between the flux estimation and the size of the burnt areas. Therefore, the flux

value depended exclusively on the sources of colonisers and the dispersal constraints of the species, but not on a characterising attribute of the fires themselves. a_j is the attribute of each of the nodes in the original species distribution (before the wildfires, n = 945), corresponding to a probability of species occurrence. nl_{ij} is the minimum number of links needed to reach node i from node j. Using PC, the amount of dispersal flux is calculated as:

$$Flux_{k, PC} = \sum_{i \neq j}^{n} a_i \cdot a_j \cdot p_{ij}^* \qquad (2)$$

where a_i i a_j are defined as above and p_{ij}^* is defined as the maximum product probability of all of the possible paths between patches i and j (including direct dispersal between the two patches).

Both metrics represent the contribution, in terms of the amount of flux, of a particular habitat patch to overall landscape connectivity (Saura and Rubio, 2010).

Data analysis

We conducted two analyses to investigate the effect of three factors: connectivity, size of the burnt patch and time since fire, on the post-fire colonisation process of the ortolan bunting (see table 1 for a summary of the data used in each analysis). First, we selected wildfires that occurred between 2000 and 2005 (n = 42) and census information from two consecutive years (2006 and 2007) and analysed the occurrence (presence or absence) of the ortolan bunting in transects conducted within the burnt areas by performing generalised linear models (GLMs) with a binomial error and a logit link function. We considered that the species was present in a transect when it was detected in either of the two survey visits. The amount of dispersal flux received in each burnt site, the burnt area (ha) and the age of the selected burnt locations (whether they occurred before or after 2004) were used as fixed factors. Quantitative variables were standardised to have a mean of zero and stan-

TABLE 1

Summary of the data used in each analysis conducted in the present study.
[Resumen de los datos utilizados en cada uno de los análisis efectuados en el presente estudio.]

	ANALYSIS 1	**ANALYSIS 2**
Statistical analysis	GLM	GLMM
Sample size	42	19
Fieldwork data	Two consecutive years	First three years after fire event
Response variable	Presence/Absence	Presence/Absence
Independent variables	– Amount of flux – Burnt area – Times since fire (before/after 2004)	– Amount of flux – Burnt area – Nº years elapsed since fire

dard deviation of one. This allowed the effect sizes of variable coefficients to be compared (Zuur *et al.*, 2009). Model fit was assessed by obtaining a Pearson's correlation coefficient, r, of the observed *vs* predicted values, providing an indication of how closely the two sets of values agree. We performed one model for each of the two connectivity metrics used (Flux$_{IIC}$ and Flux$_{PC}$).

We also conducted a second analysis with a smaller number of burnt sites from which bird information was collected during the first three years after the fire (for fires that occurred in 2005 and 2006, n = 19). We used the same response variable as in the first analysis but we focused on the temporal variation of species occurrence in selected burnt sites. The amount of dispersal flux received in each burnt site, the burnt area (ha) and the number of years elapsed since fire were used as fixed factors. All variables were standardised to allow coefficient comparisons. Additionally, the burnt site was entered as a random factor in the regression model in order to account for the dependency between data obtained in different years in the same sites by conducting generalised linear mixed models (GLMMs). Model fit was assessed as explained above. We performed one model for each of the two connectivity metrics used (Flux$_{IIC}$ and Flux$_{PC}$). All statistical analyses were undertaken using the R statistical package version 2.12.2 (R Development Core Team, 2010). GLMMs were fitted using the package MASS version 7.3-7 (Venables and Ripley, 2002).

Finally, we computed Moran's I autocorrelation test to check for spatial autocorrelation of residuals, to ensure that the occurrence patterns were spatially independent (Legendre *et al.*, 2002). We used wildfires occurring between 2000 and 2005 (n = 42) and the species occurrence in 2006 and 2007 in this analysis. We used this information because it is the most consistent regarding the fire sites and the year when census were conducted.

In addition, it considers most of the burnt sites used in the present paper. We used the UTM of each wildfire (centroid point) as the spatial coordinate and defined nine distance classes according to the median and maximum breeding dispersal distance (12 km and 45 km, respectively) observed in a Norwegian population (Dale *et al.*, 2005, 2006). These distance classes were: 0-6 km, 6-12 km, 12-18 km, 18-24 km, 24-30 km, 30-36 km, 36-42 km, 42-48km, >48 km. We analysed separately bird data recorded in 2006 and 2007. Significance was tested using 500 permutations. The results showed that correlograms were not significant (p > 0.05) neither globally nor considering each of the distance classes. These results allowed us to fit the models without explicitly considering the spatial autocorrelation among fire sites.

RESULTS

Occurrence patterns of ortolan buntings in post-fire areas

We found a high spatial heterogeneity in the patterns of ortolan bunting occurrence (fig. 1). Using the bird census data collected in two consecutive years (2006 and 2007) within the sites burnt between 2000 and 2005 (42 distinct locations), the ortolan bunting was recorded at eight different wildfire sites, mostly located on the central plateau (fig. 1). At seven of these sites, we detected the species both in 2006 and in 2007 with a tendency for the species to be more common in 2007, including its detection at an additional burn site.

Using the species information obtained in the burnt areas monitored during the first three years after fire event (19 fires that occurred in 2005 and 2006), we found that ortolan buntings became progressively more likely to appear over time, but this varied considerably. One year after the fire, the species was recorded in only one out of the nineteen burnt areas. Two

Results of generalised linear models of the occurrence of ortolan bunting on wildfires occurring from 2000 and 2005 (n = 42).
[Resultados de los modelos lineales generalizados de la presencia del escribano hortelano en zonas incendiadas entre 2000 y 2005 (n = 42).]

		Estimate	*SE*	*P*	*r*	*df*
IIC					0.91	38
	$Flux_{IIC}$	2.85	0.51	**<0.001**		
	Area	0.28	0.1	**0.005**		
	Age	–0.79	0.43	0.067		
PC					0.79	38
	$Flux_{PC}$	2.44	0.36	**<0.001**		
	Area	0.51	0.11	**<0.001**		
	Age	–1.44	0.52	**0.005**		

We performed one model for each of the two connectivity metrics used in the present study (IIC and PC). Models were run using the amount of dispersal flux, the burnt area and whether the fire occurred before or after 2004 (Age). Bold p-values indicate significant variables. Model fit was assessed using a Pearson correlation (r) of observed *vs* model-predicted values. Degrees of freedom (df) used in the analyses also shown.
[Se realizó un modelo para cada uno de los índices de conectividad utilizados en el presente estudio (IIC y PC). En cada modelo se utilizó como variables independientes la cantidad de flujo de dispersión, el área quemada y si el incendio ocurrió antes o después del 2004. Los p-valores de las variables estadísticamente significativas están destacados en negrita. El ajuste del modelo se calculó utilizando la correlación de Pearson (r) entre los valores observados y los valores predichos por el modelo. Finalmente, también se muestran los grados de libertad de los modelos.]

years after the fire the species remained in that site, showing an increase in the total number of transects where the species was detected (4 transects in 2006 versus 10 transects in 2007), and was additionally detected in two new sites. Finally, three years after the fire, the species was present in a new site and expanded to new transects within the same wildfires where it was recorded the previous year.

Influence of connectivity, patch size and time since fire on species occurrence in the studied sites

The occurrence of the ortolan bunting on sites burnt between 2000 and 2005 (n = 42) was significantly related to the amount of dispersal flux received from sources of colonisers and to the burnt area (table 2 and fig. 3).The greater the amount of dispersal flux received, the higher the probability of species occurrence (fig. 3a). The probability of species colonisation was also higher in larger burnt areas (fig. 3b) although this relationship was weaker than that established between occurrence and the estimated dispersal flux (table 2). The same result was obtained when we removed the largest wildfire (*Sant Llorens Savall*, fire code = 14) from the analysis (results not shown). This site had a much larger burnt area than the other sites and so could have biased the results. In addition, species occurrence was significantly re-

lated to whether wildfires occurred before or after 2004, decreasing in fires that occurred after 2004 (table 2). Finally, both connectivity indices (IIC and PC) showed similar results (table 2).

We found similar results when we analysed species occurrence on the 19 burnt locations from which bird information was collected the first three years after fire, mainly when using PC connectivity index (table 3). The probability of species occurrence was significantly related to the amount of dispersal flux, the burnt area and the time elapsed

since the fire (table 3). The greater the number of years since a fire the higher the probability of species occurrence, especially on those sites where the species was present in previous years.

DISCUSSION

Our results showed strong spatial differences in the post-fire occurrence of the ortolan bunting. The pattern of species occurrence was primarily associated with
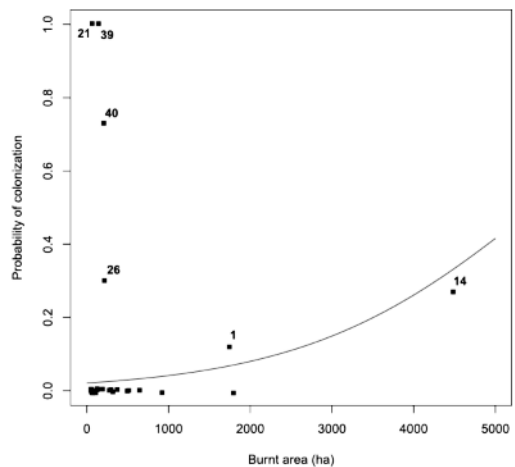
a)
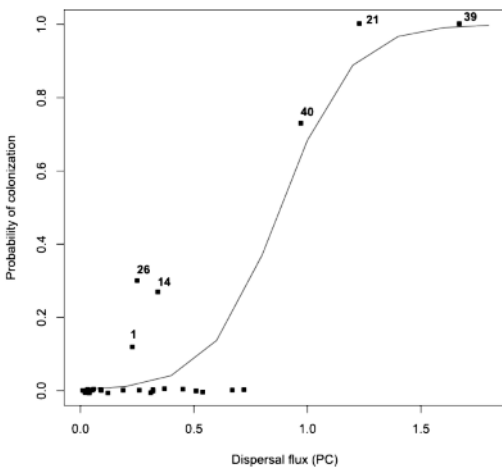
b)

FIG. 3.—Results from generalised linear models of the occurrence of ortolan bunting on sites burned before 2004. Solid lines represent predictions from (a) the amount of dispersal flux and (b) the burnt area in the full model (with other explanatory variables held at mean values). Squares represent raw data (values have been jittered to show overlapping squares). We used the results from the Probability of Connectivity (PC) as an example. Numbers correspond to wildfire codes where the species was found (see Appendix 1).
[Resultados de los modelos lineales generalizados de la presencia del escribano hortelano en sitios quemados antes de 2004. Las líneas continuas representan las predicciones de (a) la cantidad del flujo de dispersión y (b) el área quemada en el modelo completo (manteniendo otras variables explicativas en valores medios). Los cuadrados representan los datos crudos (separando ligeramente los cuadrados para mostrar valores que solapan). Hemos utilizado como ejemplo los resultados del índice de conectividad P. C. Los números corresponden a los códigos de las áreas incendiadas donde se registró a la especie (véase Apéndice 1).]

TABLE 3

Results of generalised linear mixed models of the occurrence of ortolan bunting on wildfires occurring in 2005 and 2006 (n = 19).
[Resultados de los modelos lineales generalizados mixtos de la presencia del escribano hortelano en zonas incendiadas en 2005 y 2006 (n = 19).]

	Estimate	*SE*	*P*	*r*	*df*
IIC				0.70	14
Fixed effects					
$Flux_{IIC}$	4.27	2.28	0.07		
Area	–0.49	0.92	0.60		
Time since fire	0.85	0.08	**<0.001**		
Random effects					
Fire Site		1.27			
PC				0.75	14
Fixed effects					
$Flux_{PC}$	2.47	0.35	**<0.001**		
Area	0.87	0.33	**0.02**		
Time since fire	0.85	0.08	**<0.001**		
Random effects					
Fire Site		0.71			

We performed one model for each of the two connectivity metrics used in the present study (IIC and PC). Models were run using the amount of dispersal flux, the burnt area and the number of years elapsed since fire. Bold p-values indicate significant variables. Model fit was assessed using a Pearson correlation (r) of observed *vs* model-predicted values. Degrees of freedom (df) used in the analyses and standard deviation of the random factor also shown.
[Se realizó un modelo para cada uno de los índices de conectividad utilizados en el presente estudio (IIC y PC). En cada modelo se utilizó como variables independientes la cantidad de flujo de dispersión, el área quemada y el número de años transcurridos tras el paso del fuego. Los p-valores de las variables estadísticamente significativas están destacados en negrita. El ajuste del modelo se calculó utilizando la correlación de Pearson (r) entre los valores observados y los valores predichos por el modelo. Finalmente, también se muestran los grados de libertad de los modelos y la desviación estándar del componente aleatorio.]

the amount of dispersal flux received from sources of colonisers and to a lesser extent with the amount of suitable habitat created by the fire itself, suggesting that the connectivity between habitat patches plays a major role in the colonisation of recently burnt areas. These results support the predictions from metapopulation theory that the colonisation process is greatly constrained by the connectivity of the habitat patch network (Moilanen and Hanski, 2001). They also build on pre-vious findings on birds in dynamic landscapes, suggesting that dispersal and landscape context are important factors in determining post-disturbance coloniser structure in bird communities (Brotons *et al.*, 2005).

Wildfires generate the habitats needed by open-terrain bird species such as the ortolan bunting by providing resources such as nest sites, food or lower risks of predation (Pons and Prodon, 1996; Dale and Olsen, 2002). However, we have shown that the geographi-

cal location of the new burnt sites and the limited breeding dispersal capacity of the ortolan bunting determine the colonisation process. This result explains the absence of the species in wildfires located *c.* 50 km from the nearest potential sources of colonisers [e.g. as in *Granja d'Escarp* (fire code 37) or *Caldes de Malavella I and II* (fire codes 6 and 7 respectively)] (see fig. 1) and its occurrence in burnt sites where this distance was the order of few kilometres (e.g. *Cardona*, fire code 10). For a species such as the ortolan bunting that relies on the availability of patchy and dynamic habitats, such as those created after fire (Brotons *et al.*, 2008), dispersal capability is crucial to locating areas in which to establish breeding territories and is a key factor in the overall dynamics of its distribution.

Pons and Bas (2005) showed that fire extent was an important factor determining both species richness and composition within a burnt area. Our results suggest that fire extent appeared to have an important but secondary role in determining post-fire colonisation. Patch size is expected to have a role in the post-fire colonisation process since stochastic dispersal events may be more probable in large patches. This is probably because they are more likely to be found by migrants. However, in the case of the ortolan bunting this effect was largely overridden by the effect of connectivity and dispersal pressure. Thus, although large fires may play a critical role in seeding new populations by creating large favourable habitat patches, we have shown that these areas should be connected by dispersal to population sources. In the event that they are colonised, large burnt areas may act as population reservoirs, playing an important role in determining future distribution changes.

Our results also indicated that the probability of species occurrence increased with the number of years elapsed since the fire event. This might be due to new immigrants arriving at the burnt locations or to local recruitment within burnt sites. The data analysed here may be insufficient to establish which of these hypotheses is feasible, due to the short duration of the study and/or the low species occurrence at the selected sites. Nevertheless, the fact that several of the burnt sites occurring in 2003 located close to the main species population on the central plateau [e.g. *Talamanca* (Fire code = 13) and *Castellbell* (Fire code = 15)] (personal observations) were colonised in 2008 suggests that the hypothesis of new colonisations is likely to apply in several cases. The colonisation process might be constrained by stochastic factors that are not entirely ensured in highly connected patches. For instance, mate scarcity in the new habitats may prevent effective settlement of males immediately after a fire. Time since fire may contribute to effective individual settlement and boost effective colonisation as a result of attraction by conspecifics (Dale *et al.*, 2006). On the other hand, colonisation might also be limited by vegetation regrowth. Nevertheless, the ortolan bunting is a typical pioneer coloniser of the early stages of vegetation succession and many studies have already detected it the first year after a fire (Pons and Prodon, 1996; Herrando *et al.*, 2002; Brotons *et al.*, 2005, Pons and Bas, 2005). Since all fires occurred in the early months of the year, areas sampled one year after fire have considerable vegetation regrowth ranging from 20 to 80 % of vegetation cover at 0-0.25 m height (own unpublished data). This being so, species colonisation with time elapsed since a fire may not be related to vegetation regrowth but rather to a matter of the species capacity to arrive at the recently created suitable habitat (dispersal constraints *sensu* Brotons *et al.*, 2005). We highlight the importance of long-term studies for a better understanding of this process.

Finally, in a context of global change it seems of utmost importance to extend this study to other Mediterranean species in order to understand and to be able to predict the

patterns of biodiversity change and their interactions with disturbances and ecosystem pressures on sufficiently large spatial and temporal scales. Further insights may be obtained through direct monitoring of the actual dispersal patterns (radiotracking, mark-release-recapture) of selected individuals of these disturbance-sensitive species. This may allow closer and more detailed insights into the factors limiting and enhancing colonisation and habitat use in burnt areas.

Use of connectivity indices

This paper highlights the importance of using connectivity measures to predict species distribution in a changing landscape. Thus, models based exclusively on the amount of habitat will not be realistic for species such as the ortolan bunting if they do not explicitly include its dispersal capacity. This is a key assumption incorporated into habitat– or niche-based static distribution modelling to predict changes in species distribution under scenarios of environmental change (Guisan and Thuiller, 2005). The prediction of species distributional responses to disturbances should explicitly include dispersal constraints and the context in which they occur, in order to be able to mimic observed patterns. One possibility is to integrate habitat models and information generated by using graph theory analysis, such as the amount of dispersal flux received, as estimated through metrics like IIC and PC, which, among others, may be particularly suited for these purposes (Saura and Pascual-Hortal, 2007; Saura and Rubio, 2010; Visconti and Elkin, 2009). In general, graph models offer a versatile and flexible representation of habitat mosaics and can provide insights into a variety of ecological questions at both the patch and landscape level (Urban *et al.*, 2009). Our results, together with other recent researches (McRae and Beier, 2007; Neel, 2008), contribute to demonstrating the ability to explain relevant ecological processes through a graph representation of the landscape.

This should not however preclude the value and usefulness of other available connectivity metrics and approaches. For instance, spatially explicit metapopulation models (e.g. Hanski, 1999; South, 1999) are able to consider the population dynamics associated with individual habitat patches and with an explicit modeling of birth, mortality, emigration and immigration processes. Although the graph metrics used here were able and sufficient to capture the effects of functional isolation on colonisation patterns (absence/presence records), metapopulation models of different kinds would be needed when the connectivity analysis requires a more detailed evaluation of the demographic dynamics and temporal persistence of the target populations. This would require however that the information needed to parameterise these models is available at sufficiently wide scales to be usable for projecting biodiversity patterns under different change scenarios, which may limit in practice the scope of application of some of the available models and metrics related to landscape connectivity (Calabrese and Fagan, 2004).

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APPENDIX 1

Description of the areas affected by fire used in this study, in chronological order of burn year. The description includes the name, code, burn year, fire area, main habitat before the fire and number of line transects conducted within the burn area.

[Descripción de las áreas afectadas por el fuego utilizadas en este estudio, en orden cronológico. Se incluye nombre, código, año del incendio, área incendiada, tipo de hábitat principal antes del incendio y número de transectos lineales efectuados en el interior del perímetro del fuego.]

Fire name	Fire code	Year	Fire area (ha)	Main habitats	Number of transects
Albiol	27	2000	615.24	Shrubland	17
Camposines	32	2000	52.38	Shrubland	2
Fontrubi	22	2000	88.11	Forest (*P. halepensis*)	3
PratdeCompte	31	2000	268.56	Forest (*P. halepensis*)	13
Badalona	16	2001	66.69	Shrubland	3
Cadaques	1	2001	1685.34	Shrubland	25
Castelldefels	24	2001	54	Shrubland	2
Cubells	40	2001	212.13	Shrubland and *Quercus coccifera*	11
Escala	2	2001	374.31	*P. halepensis* and shrubland	11
LaFloresta	38	2001	71.55	Shrubland	4
VallbonaAnoia	20	2001	59.4	*P. halepensis*, *P. pinea*, shrubland and *Quercus ilex*	2
Castellbisbal02	18	2002	119.25	Shrubland	5
Tivissa	29	2002	54.63	Shrubland and *P. halepensis*	2
VilaverdLilla	25	2002	498.6	Shrubland	15
Alcover	26	2003	218.7	Shrubland	10
CaldesMalavella03	7	2003	60.21	*P. pinea* and shrubland	2
CastellbelliVilar	15	2003	308.97	Shrubland and *P. halepensis*	14
DaltmarOlerdola	23	2003	129.33	Shrubland	6
GranjaEscarp	37	2003	1845.54	Shrubland	22
Jorba	21	2003	63.63	Shrubland	3
MasanetGran	8	2003	65.88	*Q. suber*, *P. pinea*, *P. pinaster*, *Q. ilex* and shrubland	2
MasanetPetit	9	2003	963.18	*Q. ilex*, *Q. suber* and shrubland	21
Masquefa	19	2003	60.48	Forest (*P. halepensis*)	3

APPENDIX 1 (cont.)

Fire name	Fire code	Year	Fire area (ha)	Main habitats	Number of transects
PlatjaAro	4	2003	330.57	Shrubland, *Q. suber*, *P. halepensis* and *P. pinea*	12
SantFeliuGuixol	5	2003	513.72	Shrubland, *Q. suber*, *P. halepensis* and *P. pinea*	18
SantLlorensSavall	14	2003	4497.93	Forest (*P. halepensis*)	30
Selvanera	39	2003	131.31	Shrubland	5
Talamanca	13	2003	190.98	Forest (*P. halepensis*)	7
Montanissell	41	2004	81.18	Shrubland and *Pinus nigra* subsp. *salzmanni*	4
Montgri	3	2004	540.72	Shrubland	16
Balsareny	11	2005	863.64	Forest (*P. halepensis*)	19
BorgesdelCamp	28	2005	104.76	Shrubland and *P. halepensis*	3
CaldesMalavella05	6	2005	82.44	*P. pinea* and shrubland	3
Cardona	10	2005	1264.77	Forest (*P. halepensis*)	21
Castellbisbal05	17	2005	209.52	Shrubland and *P. halepensis*	6
Margalef	36	2005	393.03	*P. halepensis* and shrubland	13
PalmadeEbre	35	2005	95.85	Shrubland	4
Perello	30	2005	96.3	Shrubland	5
PobladeMasaluca	33	2005	105.3	Shrubland and *P. halepensis*	4
RibaRoja05	34	2005	613.35	*P. halepensis* and shrubland	18
Rocafort	12	2005	790.47	*P. halepensis* and shrubland	20
Viladecans	42	2005	59.22	Shrubland	3
Capmany	45	2006	264.69	Shrubland and *Q. suber*	11
Cistella	44	2006	208.8	*P. halepensis* and shrubland	7
LaFebro	48	2006	51	*P. sylvestris* and shrubland	2
Ogern	46	2006	90.81	Forest (*Pinus nigra* subsp. *salzmanni*)	4
Vandellos	49	2006	1142.55	Shrubland	21
Ventallo	43	2006	802.62	Forest (*P. halepensis*)	20
Vimbodi	47	2006	117.18	*P. halepensis* and shrubland	5