

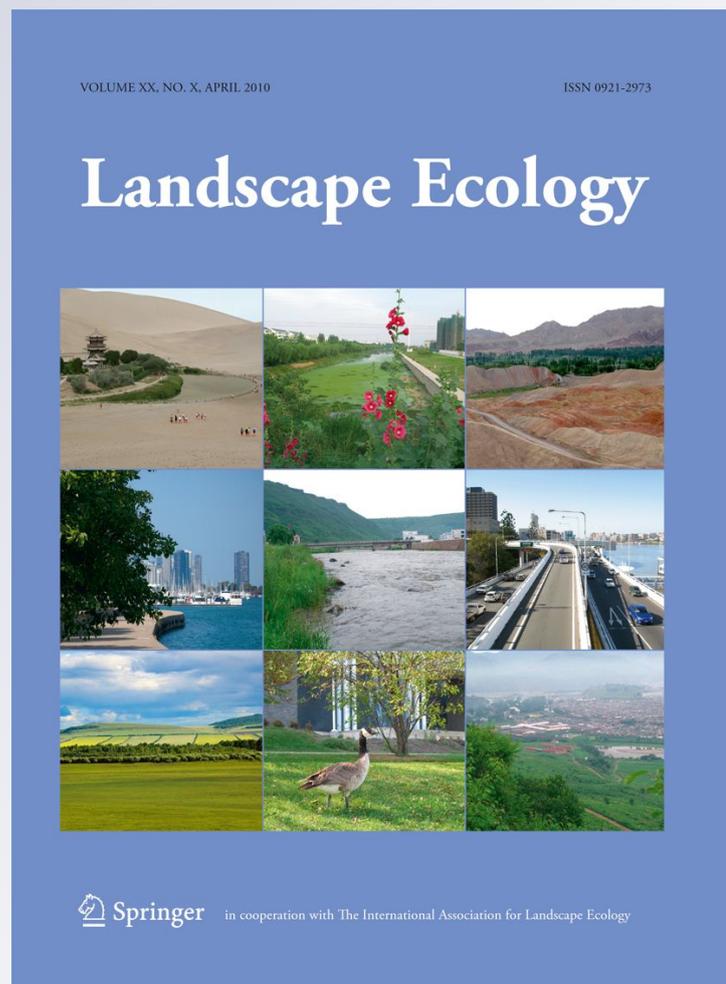
Recent fire history and connectivity patterns determine bird species distribution dynamics in landscapes dominated by land abandonment

Elena L. Zozaya, Lluís Brotons & Santiago Saura

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Recent fire history and connectivity patterns determine bird species distribution dynamics in landscapes dominated by land abandonment

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Abstract Mediterranean landscapes are suffering two opposing forces leading to large-scale changes in species distribution: land abandonment of less productive areas and an increase in wildfire impact. Here, we test the hypothesis that fires occurred in recent decades drive the pattern of expansion of early-successional, open-habitat bird species by aiding in the process of colonisation of newly burnt areas. The study was carried out in Catalonia (NE Spain). We selected 44 burnt sites occurring between 2000 and 2005 to model colonisation patterns under different assumptions of potential colonisers' sources and evaluated the colonisation estimates with empirical data on six bird species especially collected for this purpose. We first defined three landscape scenarios serving as surrogates of potential colonisers' sources: open-habitats created by fire, shrublands and farmlands. Then, we used a parameter derived from a functional connectivity metric to

estimate species colonization dynamics on the selected sites by each particular scenario. Finally, we evaluated our colonisation estimates with the species occurrence in the studied locations by using generalized linear mixed models. The occurrence of the focal species on the newly burnt sites was significantly related to the connectivity patterns described by both the recent fire history and the other open-habitat types generated by a different type of disturbance. We suggest that land use changes in recent decades have produced a shift in the relative importance of habitats acting as reservoirs for open-habitat bird species dynamics in Mediterranean areas. Before the middle of the twentieth century species' reservoirs were probably constituted by relatively static open habitats (grassland and farmland), whereas afterwards they likely consist of a shifting mosaic of habitat patches where fire plays a key role as connectivity provider and largely contributes to the maintenance of species persistence.

E. L. Zozaya (✉) · L. Brotons · S. Saura
Centre Tecnològic Forestal de Catalunya, Ctra. de St.
Llorenç de Morunys a Port del Comte km 2, 25280
Solsona, Spain
e-mail: elzozaya@gmail.com

L. Brotons
Institut Català d'Ornitologia, Museu de Ciències Naturals
de la Ciutadella, Passeig Picasso s/n, 08003 Barcelona,
Spain

S. Saura
Universidad Politécnica de Madrid, E.T.S.I. Montes,
Ciudad Universitaria s/n, 28040 Madrid, Spain

Keywords Colonisation dynamics · Connectivity · Fire history · Habitat configuration · Land-use changes · Land abandonment · Open-habitat bird species · Potential dispersal flux

Introduction

Conservation of species diversity at local, regional, and continental scales has received increasing attention as

human pressures and modification of ecosystems increase. Much of the research has focused on the effects of habitat loss and subsequent landscape fragmentation on species dynamics (e.g. Villard et al. 1999; Alderman et al. 2005). Nevertheless, in some cases, species responses appear to be more complex than initially expected because the impacts of current landscape change interact with previous changes in land use affecting those landscapes (de Blois et al. 2001; Kiss et al. 2004; Kuussaari et al. 2009). This is for instance the case of the effect of past agricultural use on present plant communities in temperate and tropical forests (Dupouey et al. 2002; Heckenberger et al. 2003; Dambrine et al. 2007) or on current stream biodiversity (Harding et al. 1998), where past land uses have long lasting impacts on present biodiversity patterns.

In this context, historical landscape structure is also expected to influence present species diversity since it affects landscape connectivity. If landscape structure is altered but local populations at the site are maintained, sites with high historical connectivity may maintain a high diversity in comparison with sites with lower historical connectivity (Lindborg and Eriksson 2004). Therefore, we expect to find a strong signal of previous landscape changes on present species distribution dynamics, especially in colonisation patterns of new habitats (Hanski 1999).

Since the middle of the twentieth century, important and rapid changes have occurred in Mediterranean ecosystems affecting the availability and the spatial arrangement of open habitats. On one side, a growing demand for higher economical productivity and population concentration in the cities has prompted two contrasting processes: land use intensification in areas most favourable to agriculture and abandonment of areas with a marginal productivity (Bouma et al. 1998; Russo 2007). On the other side, wildfires frequency and extent have increased due to fuel accumulation after the abandonment of rural traditional activities (e.g. firewood extraction), the influence of climate change and the more numerous ignition sources (Piñol et al. 1998; Pausas 2004). Whereas the expected consequence of agricultural abandonment is the reduction of the extent of open spaces with a concurrent regrowth and expansion of woodlands through natural succession (Preiss et al. 1997; Moreira et al. 2001), fires are expected to have the opposite effect by creating new habitats, maintaining the availability of open patches (Lloret et al. 2002). These

counteracting events might have important consequences in the dynamics of the species by modifying the processes providing suitable habitats for them. In the past, the distribution dynamics of these species were probably linked to the presence of relatively static habitats (farmland and grazed grasslands and shrublands). However, with the marked increase in fire footprint in the landscape and the vegetation closure (resulting from rural land abandonment), recently burnt areas may play a key role in creating suitable habitats for open-habitat species and thus in species dynamics (Brotons et al. 2008; Vallecillo et al. 2009).

In this study we evaluated the effect of recent fire history on species dynamics at large spatial and temporal scales using Mediterranean landscapes and early-successional, open-habitat bird species as study models. The aim of this study was to test the hypothesis that species colonisation of newly burnt areas is greatest in those areas connected by dispersal to previously burnt areas. We focused in the region of Catalonia and selected six bird species that have strong preferences for open-habitat types, like farmlands and/or shrubland, and make extensive use of recently burnt areas in relatively high densities (Pons and Prodon 1996; Herrando et al. 2002; Pons and Bas 2005). We specifically address three questions: (1) which is the role of recent fire history on the colonization of new burnt areas by open-habitat bird species? (2) How long do the consequences of fire impacts determine current colonization patterns? (3) Which is the role of more static open-habitat types, such as farmlands and shrublands, on the post-fire colonization patterns? Finally, since open habitats are not randomly distributed in the study region but depend on factors such as slope, orientation and historical factors (e.g. Díaz-Delgado et al. 2004a, b), we additionally addressed the hypothesis that colonisation is also shaped by such limitations by explicitly incorporating a regional factor. With this aim, we defined three different regions in Catalonia differing broadly in climatic patterns and dominant forest species (derived from DGMN 1994 and Burriel et al. 2000) (Fig. 1).

Methods

Study region and site selection

The study was conducted in Catalonia, a region dominated by Mediterranean climate and located in

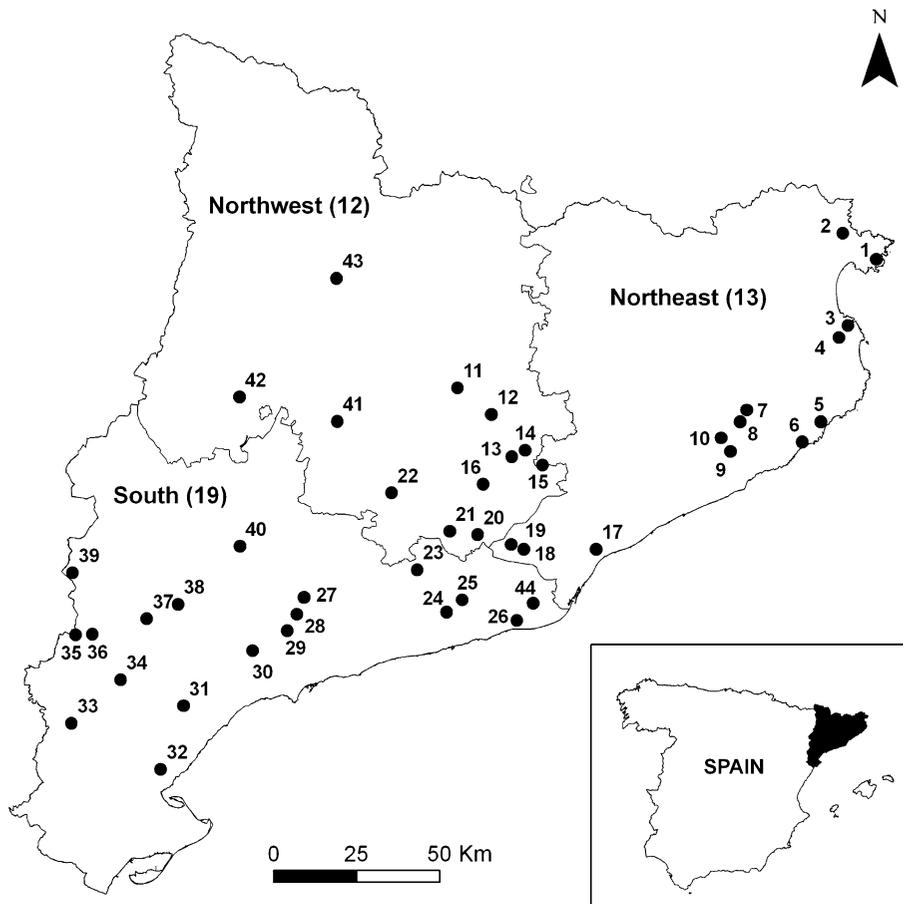


Fig. 1 Geographical location of the 44 studied burnt areas in the map of Catalonia. The three defined regions, showing the total number of fires. The map on the *lower right* shows the location of the study region (Catalonia) in *black*

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 2005, resulting in 44 sites (Fig. 1). These locations represent the new suitable habitats patches for open-habitat bird species during that time period, thus capturing landscape dynamics. We selected these burnt areas in order to estimate the post-fire colonisation patterns under different assumptions of potential colonisers' sources and evaluate our predictions using fine-grained bird data specifically gathered for this purpose (see following sections). Fire perimeters were provided by the *Departament de medi ambient i habitatge* (DMAH) of the Catalan government.

Selected wildfires ranged from 52 to 6,278 ha 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 or Holm Oak forests] and shrubland mosaics containing open habitats (clearings, 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.

Focal species

This work focused on six open-habitat bird species with variable preferences for open-habitats types in Mediterranean landscapes (Estrada et al. 2004): the Corn Bunting (*Emberiza calandra*) and the Black-eared Wheatear (*Oenanthe hispanica*) with a strong preference for farmland areas, the Tawny Pipit (*Anthus campestris*) and the Thekla Lark (*Galerida*

theklae) that mainly select shrubland areas, and the common Linnet (*Carduelis cannabina*) and the Woodlark (*Lullula arborea*) that occupy all kind of open-habitats. In addition, all these species have been associated with recently burnt areas (Pons and Prodon 1996; Herrando et al. 2002). Therefore, all can potentially occur during the first years after fire in burnt shrubland, in burnt forest or in both. Furthermore, they were detected in more than 25% of the newly burnt sites, thus providing sufficient data to tackle the above mentioned research questions.

Post-fire bird data

We used bird data from a monitoring program described by Zozaya et al. (2010) investigating bird species responses to recent wildfires in Catalonia. Within each fire perimeter a number of line-transects are established. Each line transect lasts 15 min and covers approximately 500 m. 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, 25–50, 50–100 and >100 m). Transects are conducted entirely across burnt wildland avoiding unburnt patches (forest or farmland) and fire edges. The number of transects per fire is a linear function of the logarithm of fire area. In the largest burnt areas, transects are distributed in a number of representative locations covering habitat heterogeneity within fire perimeter. Additionally, the minimum distance between two transects and between transects and fire edge is 150 and 50 m respectively. Finally, bird surveys are conducted once every breeding season (10th May–15th June), by experienced ornithologists at a speed of 2 km/h approximately, 3 h after sunrise and under good weather conditions (i.e. without rainfall or strong wind) (Bibby et al. 2000).

In this work we used bird surveys conducted in 2006 and 2007 in the studied fires and noted the occurrence (presence or absence) of the focal species within 100 m belts on both sides of the track.

Estimation of postfire colonisation patterns under different landscape scenarios

We identified three scenarios characterized by the cover type that may act as the source habitat (shrubland or farmland), and in the case of the shrublands by

the type of disturbance that generates the shrub cover (fire or others) (Fig. 2). For each scenario, we selected the 4 × 4 km squares in which the abundance of the corresponding open habitat type was higher than 50 ha (the minimum amount of suitable habitat where species population was considered sufficient to provide immigrants). We used the land use map of Catalonia of 1997 (just before the occurrence of the selected burnt sites) to construct these scenarios. The following scenarios were analysed (see also Fig. 2):

- (1) Shrubland associated to fire (*fire scenario*). This scenario corresponds to the areas covered by shrubs within wildfires that affected Catalonia the last 20 years of the twentieth century. We separated fires from different periods to allow the identification of potential long-term responses: (a) *from 1980 to 1999* (193,000 ha of shrubland, corresponding to 431 squares), (b) *from 1980 to 1989* (96,000 ha, representing 263 squares) and (c) *from 1990 to 1999* (97,000 ha, corresponding to 251 squares). Fire perimeters were provided by the DMAH for the period 1986–1999 and by the Centre recerca ecològica i aplicacions forestals (CREAF) for fires that occurred between 1980 and 1985. In the case of the areas affected by wildfires occurred between 1998 and 1999 and since the land-use map of 1997 characterizes these areas with the land-use previous the fire event, we assumed that all burnt wildland became shrubland after the fire (Lloret et al. 2002).
- (2) Non fire-related *shrubland scenario*. This corresponds to shrub areas not affected by fire. They may have been originated from other landscape processes such as vegetation succession after the abandonment of agricultural lands or growth limitation due to site conditions. These shrubland areas have not suffered any fire in the last 20 years of the twentieth century although they could have been affected by this disturbance earlier on. In total, the shrubland scenario accounted for 663,000 ha (corresponding to 1,709 squares).
- (3) *Farmland scenario* corresponded to the non-irrigated cereal crops present in the study region. We used this habitat type and did not include other farmland habitats, such as vineyard and fruit trees, because all the studied species used cereal crops but not other type of irrigated or intensive farmland (Estrada et al. 2004). In total,

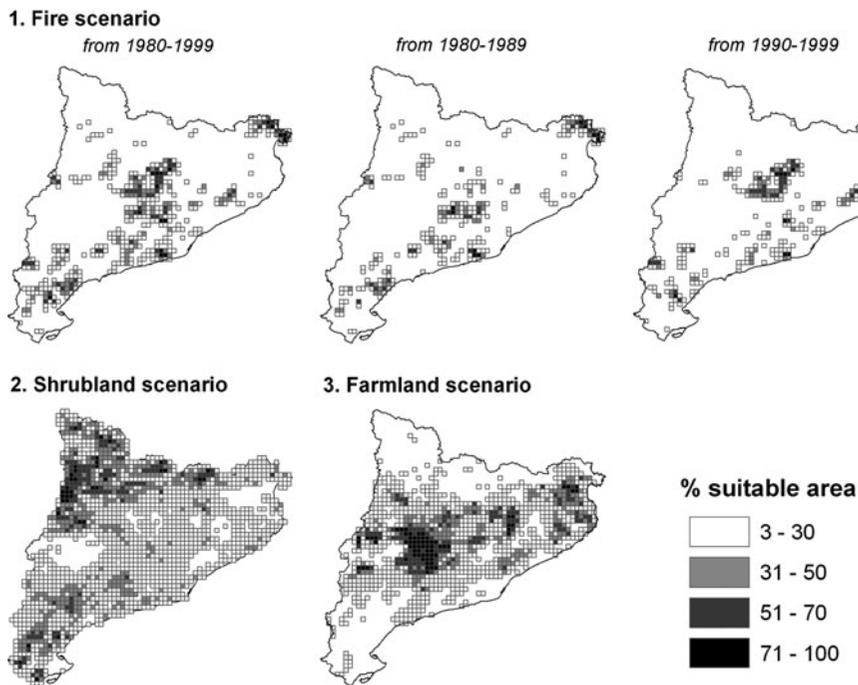


Fig. 2 Landscape scenarios used to examine colonisation patterns of six open-habitat bird species in recently burnt areas. Fire scenario was divided in three different time periods in order

to allow the identification of potential long-term responses. Each landscape scenario is characterized by the percentage of suitable habitat

the farmland scenario accounted for 472,000 ha (representing 1,096 squares).

For each landscape scenario described above we used a graph theory-based approach in order to estimate the amount of dispersal flux received in the newly burnt sites as a measure of the species capacity to colonise these sites. Hence, burnt areas receiving great amount of dispersal flux will have greater ability to be colonised by open-habitat bird species. According to this theory, a landscape ('graph') is conceived as a set of habitat patches ('nodes') and connecting elements ('links'). 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 directly disperse between two habitat patches. This will depend on the distance between habitat patches and the species capacity of dispersal. In this sense, we did not find accurate information on the dispersal ability for any of the focal species and for this reason we used available data on another early-successional bird

species, the Ortolan Bunting (*Emberiza hortulana*) as reported by Dale et al. (2005). In their study, they investigated individual movements of a whole population in Norway and found a median dispersal distance of about 12 km. Assuming that the dispersal distance of early-successional bird species might be relatively similar (considering the similar functional role, behaviour and body mass they present) (Paradis et al. 1998), we used this distance as a reference of the dispersal abilities of all the studied species.

We differentiated two types of nodes: (1) the nodes comprising the sources of colonisers (different in each landscape scenario) and (2) the nodes corresponding to the new suitable habitat patches originated after the studied wildfires ($n = 44$). Additionally, in order to characterize the links we used centroid-to-centroid Euclidean distances between nodes and a median dispersal distance of 12 km. Finally, links are here considered symmetric, i.e. the probability of dispersal from patch i to patch j is the same than from patch j to patch i .

Once we established the matrices of nodes and distances for each of the scenarios we estimated the

amount of dispersal flux received in each of the recently burnt sites by using a connectivity index named the probability of connectivity (PC) (Saura and Pascual-Hortal 2007), implemented in Conefor Sensinode software (CS) (Saura and Torné 2009, <http://www.conefor.org>). This index is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other given a set of n habitat patches and the links among them (Saura and Pascual-Hortal 2007). In this sense, PC relies on a probabilistic connection model (there is a certain probability of direct dispersal between patches i and j , p_{ij}). In this study, a probability of direct dispersal $p_{ij} = 0.5$ was set for the reference dispersal distance (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). In particular, we used the flux fraction of the PC index (Saura and Rubio 2010) and measured the amount of dispersal flux in a given recently burnt area (k) as:

$$dPCflux_k = \sum_{i \neq j}^n a_i \times a_j \times p_{ij}^* \quad (1)$$

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 newly 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 colonisers' sources and the dispersal constrains of the species, but not on a characterising attribute of the fires themselves. a_j is the attribute of the nodes in each of the landscape scenarios (before the analyzed wildfires), corresponding to the percentage of suitable area. 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) (Saura and Pascual-Hortal 2007; Saura and Rubio 2010). This $dPCflux_k$ metric represents 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 generalized linear mixed models (GLMM) to analyze the role of the described scenarios

on the colonisation process of the selected species. We used the occurrence (presence or absence) of each species in transects conducted on burned areas as the response variable in a model with a binomial error and a logit link function. We considered that a given species was present in a transect when it was detected in any of the two survey-visits. The amount of dispersal flux was used as a fixed factor. Additionally, we explicitly considered the size of the burnt areas as a fixed factor, because it is known to influence post-fire colonisation processes (Pons and Bas 2005). Including this variable we also took into account the greater sampling effort made in the largest fires. Area was log-transformed in order to prevent skewed distribution. On the other hand, site was entered as a random effect in the regression model to account for the correlation between observations made in the same site, which can lead to non-independent error structure in the data. A P -value of <0.01 was used to indicate significance in all statistical tests (Zuur et al. 2009). Model fit was assessed by obtaining a Pearson's correlation coefficient, r , of the observed versus predicted values, providing an indication of how closely the two sets of values agree.

Furthermore, when we did not find a significant relationship between landscape scenarios and post-fire colonisation patterns, we analyzed the interaction of the amount of dispersal flux and a regional factor in order to evaluate whether significant response on species dynamic might be hidden by an effect of regional variability originated by historical and environmental factors. With this aim, we divided Catalonia in three different regions (South, Northwest, Northeast) based on differences in climate and dominant forest species (derived from DGMN 1994 and Burriel et al. 2000) (see Fig. 1; Table 1). Each region has been distinctly affected by wildfires in the last decades (Díaz-Delgado et al. 2004a). The performance of the model and model fit was assessed as in the previous analysis. All statistical analyses were undertaken in 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).

Results

We found differences between species in the number of colonised burnt sites, indicating a large

Table 1 Characterization of the three regions considered in the study in Catalonia according to mean annual temperature (*T*), mean annual precipitation (*P*), and dominant forest tree species

Region	Mean annual <i>T</i> (°C)	Mean annual <i>P</i> (mm)	Dominant forest tree species
South	14.41	533.91	<i>P. halepensis</i> , <i>Quercus ilex</i> , <i>P. nigra</i>
Northwest	10.00	810.42	<i>P. sylvestris</i> , <i>P. nigra</i> , <i>Q. ilex</i> , <i>Q. humilis</i>
Northeast	13.02	841.99	<i>Q. ilex</i> , <i>Q. humilis</i> , <i>P. sylvestris</i> , <i>Q. suber</i>

Data are from DGMN (1994) and Burriel et al. (2000)

heterogeneity in the species capacity to colonise recently burnt areas. The most common species (occurring in more than 25 locations) were the Woodlark, the common Linnet and the Black-eared Wheatear, followed by the Thekla Lark, the Corn Bunting and the Tawny Pipit (Fig. 3). Additionally, most of the colonised sites were distributed between the South and the Northwest regions, whereas few sites were colonised in the Northeast region, suggesting an effect in post-fire colonisation process of factors acting at regional scale (Fig. 3). Following, we present the results of the three landscape scenarios explaining postfire colonisation patterns.

Fire scenario

The occurrence of all species except the Corn Bunting was significantly related to the amount of dispersal flux received from any of the scenarios described by old fires (Table 2; Fig. 4a), indicating an important role of recent fire history in species dynamics. The

probability of colonisation of the common Linnet, the Thekla Lark and the Black-eared Wheatear was significantly related to the interaction between the amount of dispersal flux received from fires occurring in the 80 s and regions, indicating that these species exhibited a significant response to the oldest fires considered in the present study; however it varied depending on the region where fires occurred, being positively related to those occurring in the Northeast region (Fig. 4a). In the case of the Tawny Pipit and the Woodlark, the wildfires occurred in the 90 s seemed to greatly influence the observed patterns in the newly burnt sites (Table 2; Fig. 4a).

Shrubland scenario

The probability of colonisation of four out of the six studied species (the common Linnet, the Thekla Lark, the Woodlark and the Black-eared Wheatear) was positively related to the landscape scenario corresponding to the shrubland areas not affected by fire

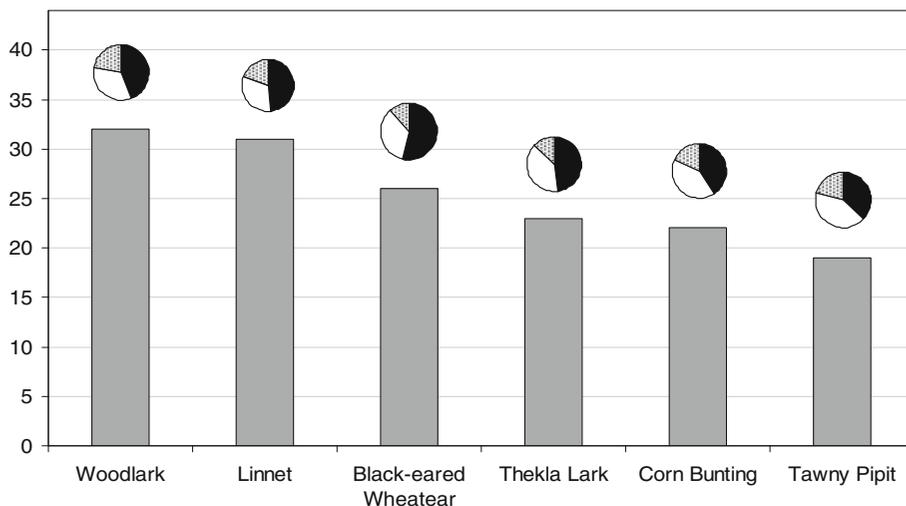


Fig. 3 Frequency distribution for the six open-habitats bird species in the 44 burnt sites and pie chart of the percentage of species presence within the South region (in black), the Northwest region (in white) and the Northeast region (black dotted)

Table 2 Results of GLMM of the occurrence of six open-habitat bird species on wildfires occurring between 2000 and 2005 ($n = 44$) according to different landscape scenarios

Landscape scenario	Tawny Pipit		Linnet		Corn Bunting		Thekla Lark		Woodlark		Black-eared Wheatear	
	P-value	r	P-value	r	P-value	r	P-value	r	P-value	r	P-value	r
Fire												
	From 1980 to 1999	<0.001	0.94									
From 1980 to 1989												
From 1990 to 1999												
Shrubland												
Farmland												

P-values are shown for those scenarios significantly related to the species observed patterns, either by themselves or by considering the interaction with the three regions defined in the study area. Model fit was assessed using a Pearson correlation (*r*) of observed versus model-predicted values
*R*_{NW} northwest region; *R*_{NE} northeast region

(Table 2; Fig. 4b). In the case of the common Linnet and the Thekla Lark, this relation depended on the region where shrubs occurred, being positively related in the South and the Northwest region (Fig. 4b). The interaction between the amount of dispersal flux and the regional factor was also significant in the case of the Tawny Pipit (Table 2), however it was negative in all regions (i.e. the greatest the amount of dispersal flux the lower the probability of colonisation), suggesting a negative effect of this scenario on this species (Fig. 4b).

Farmland scenario

The colonisation dynamics of four species (the Tawny Pipit, the Corn Bunting, the Woodlark and the Black-eared Wheatear) were significantly related to the amount of dispersal flux received from farmland areas, indicating the importance of a well connected network of agricultural areas for the dynamic of these species (Table 2; Fig. 4b). For three of these species the importance of farmland areas depended on the region where they occurred, being in all species positive in the Northwest region (Fig. 4b).

Finally, we found that for four species the greatest correlation between observed and predicted values was obtained when considering any of the fire scenarios (Table 2). This result stresses the importance of recent fire history on the studied species dynamics.

Discussion

We investigated the influence of different processes related to open habitats on the dynamics of bird species in a European-Mediterranean region. In the present Mediterranean landscape context, where wildfires are practically the most important force creating and maintaining open habitats, we focussed in the role of recent fire history on species dynamics. We surveyed open-habitat birds at 44 burnt sites selected strategically to represent the new suitable habitat patches appearing in the region, thus capturing landscape dynamics. This approach allows a direct comparison of the influence of different habitat types (shrubland and dry, extensive, farmlands) on faunal distributions. We examined its influence on six bird species. There was a strong association between

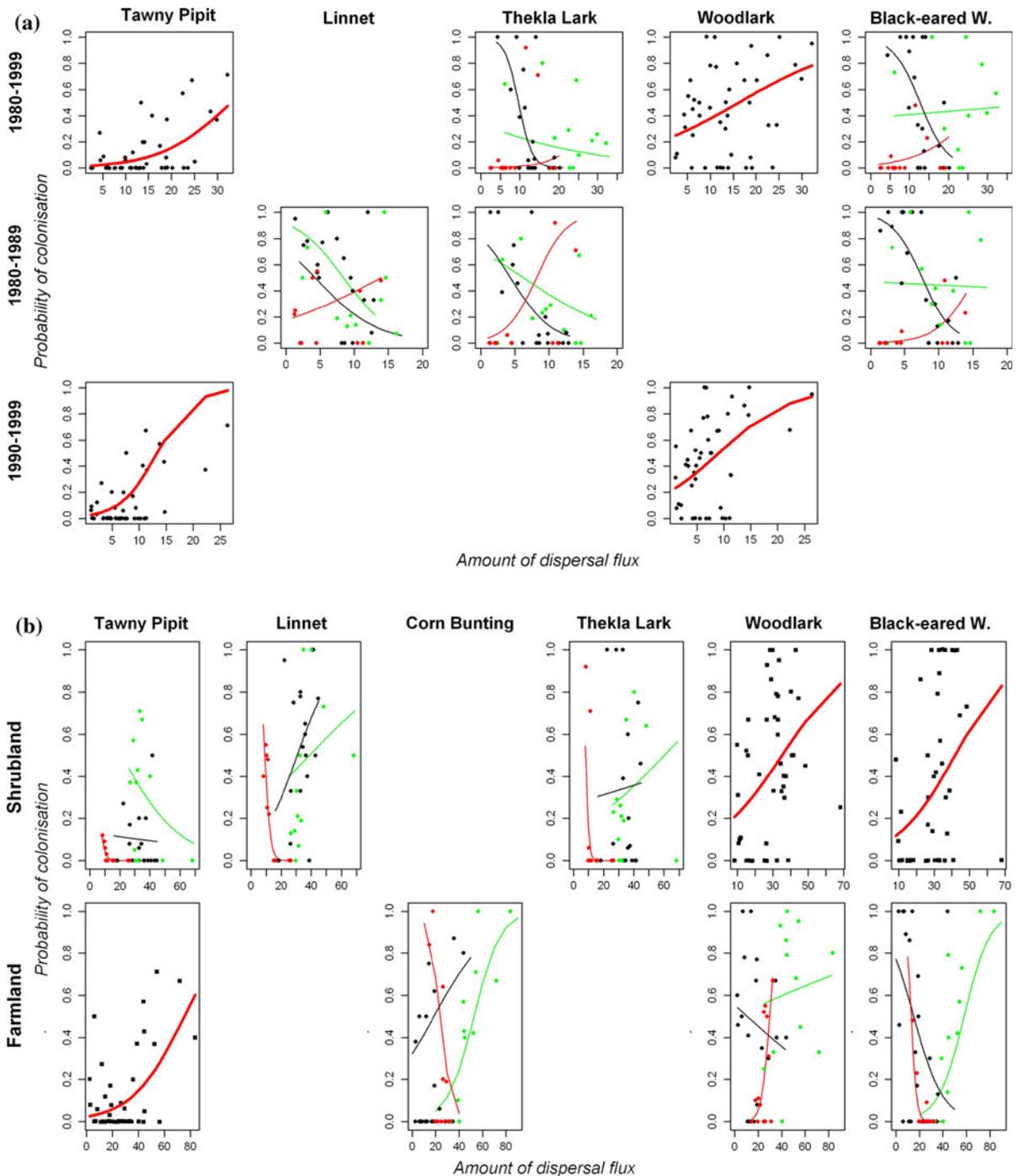


Fig. 4 Results from GLMM for the fire scenario (a) and the shrubland and farmland scenarios (b). *Solid lines* represent predictions from the amount of dispersal flux (with the size of the burnt area held at mean values). *Lines* are shown separately for the different regions when this was a significant factor in the fitted models (with *black*, *green* and *red* representing predictions

for the South, Northwest and Northeast regions respectively). *Dots* represent raw data (values have been jittered to show overlapping dots). Results are only shown for those scenarios for which the amount of dispersal flux was significantly related to the species occurrence. (Color figure online)

open-habitat birds in newly burnt areas and both recent fire history and the other open habitat types generated by a different type of disturbance.

Influence of fire regime

Fire is a key ecological process in Mediterranean-climate environments due to the combination of hot and dry summers with dense vegetation structure (Moreno and Oechel 1994). In the European part of the Mediterranean basin, the number and the size of wildfires have increased in the last decades as consequence of land-use changes and increasing climatic fire risk (Piñol et al. 1998; Díaz-Delgado and Pons 2001; Pausas 2004). This has led to an increase in the importance of this disturbance in the landscape configuration (Moreira and Russo 2007) by producing a network of habitat patches at different successional stages that has been shown to be of great importance for early-successional, open-habitat bird species (Brotons et al. 2008; Vallecillo et al. 2009). In this sense, Vallecillo et al. (2009) focused on 10 bird species (including those considered in the present work) and found that changes in species distribution between two breeding bird atlases carried out in Catalonia, one from the period 1975–1983 (Muntaner et al. 1984) and another from 1999 to 2002 (Estrada et al. 2004), are in part explained by the species occupancy of the burnt areas occurred during the time period between the two atlases. Our results are in line with their work and confirm the hypothesis that fires occurring in the last decades are acting as sources of immigrants to the new suitable habitats appearing in the landscape. Overall, the probability of colonisation of a recently burnt area was greatest in those sites well connected by dispersal to other previously burnt areas.

Furthermore, according to our results, which indicate a positive effect of the oldest fires considered in this study (10–20 years old) on current colonisation dynamics for some of the studied species, fire impact on species dynamics may be extended over relatively long periods of time. It is interesting to note that larger temporal lags may not be extended over longer periods since Mediterranean vegetation is highly resilient to fire effects (Hanes 1971; Lloret 1998) and open-habitat birds tend to disappear from disturbance sites some years after the fire event (Prodon and Lebreton 1981; Jacquet and Prodon 2009; Zozaya et al. 2011). In this case, individuals might be forced to leave the

areas and colonise new high quality ones, suggesting that wildfires might function as non-permanent colonisers' sources.

These results together with other studies contribute to explain the role of wildfires in the current dynamics of early successional, open-habitat bird species in Mediterranean areas in four distinct steps. First, wildfires generate the adequate habitat for open-habitat birds colonisation (Pons and Prodon 1996), however their colonisation depend on whether they are connected, and therefore potentially reachable, by dispersal from other previously burnt areas. Second, if these areas are colonised, they may act as sources of colonisers to other new suitable areas created as a consequence of new fires. Third, later on and as vegetation succession takes place, these areas might not be adequate for these species and these species will probably disappear (as for instance in former cork oak forest, Jacquet and Prodon 2009). Forth, since new fires are likely to occur in the same area as a consequence of the non-randomness of fire regime (Díaz-Delgado et al. 2004a, b), this area could be again colonised by these species, which at a broader scale ensures the persistence of these species in such fire-dominated areas. This cycle underlines the importance of the temporal and spatial structure of the fire regime in order to predict species dynamics (Moloney and Levin 1996).

Influence of non-fire related habitats

Fire regime does not appear to be the only factor controlling open-habitat bird dynamics. Non-burnt shrubs and farmland areas strongly contribute to explain the pattern of occurrence of open habitat birds on recently burnt areas.

Four of the six studied species were positively related to the shrubland scenario. Although certain areas in the region have been maintained as shrubs due to permanent abiotic limitations (e.g. water availability and limited soil depth), one of the greatest disturbances that have generated a huge increase in the shrub cover in the last decades is the abandonment of large areas of agricultural lands (Preiss et al. 1997). This land-use change has exerted an important effect on bird populations; with a negative effect for specialist farmland birds and a short-term positive effect on other open-habitat bird species (e.g. Sirami et al. 2008, 2010). The occupancy of these areas during the middle of the twentieth century by the

species here analysed might explain the general positive effect of this scenario on the post-fire colonisation patterns. Whilst our results indicate that land abandonment seems to favour species dynamics, it is important to note that at larger temporal scale this old agricultural areas tend to become wooded and eventually forested areas (Cramer et al. 2008), having a negative effect for the studied species, which are forced to migrate to other areas (Farina 1997). This fact might suggest that although current shrub configuration in the landscape is helping the dynamic of open-habitat species, this might not be a permanent source of individuals in the medium or long term, as also suggested in the case of old fires. Since these species are among the most threatened species in Europe (Birdlife International 2004) one option would be to manage certain shrubs in areas that may serve as connecting elements or stepping stones enhancing species dynamics and their regional persistence.

The two species that did not respond positively to the shrubland scenario were the Corn Bunting and the Tawny Pipit. The explanation could rest on species habitat preference (Sirami et al. 2008). On one hand, in Catalonia, the Corn Bunting is strongly linked to cereal cropped areas and only appears in shrubland areas if agricultural fields are imbedded within the mosaic (Estrada and Orta 2004; Vallecillo et al. 2008). On the other hand, the Tawny Pipit is strongly and negatively related to abandoned areas since it selects sparse shrubland (Aymerich and Santandreu 2004; Sirami et al. 2007).

Furthermore, the described farmland network contributed to explain the colonisation patterns of four out of the six species. Although the importance of cropped areas for feeding, foraging and breeding for the focal species is well known (e.g. Sanderson et al. 2005), our study highlights the importance of maintaining a highly connected farmland network for supporting the species spatio-temporal dynamics and persistence. This result might suggest that in spite of the global decrease of cereal cover in Catalonia during the last decades and the detrimental effect of agricultural intensification on farmland species (Mañosa et al. 1996; Brotons et al. 2004), the current network of extensively cropped areas still plays an important role as a permanent source of open-habitat birds' immigrants. Nevertheless, if the extensive farmland cover continuous to decrease, as it seems to be the current trend, processes such as habitat degradation or fragmentation, already occurring in

other European countries, might have a great negative impact on these species (Donald et al. 2001). This is of utmost importance since all the studied species have an unfavourable conservation status in Europe (BirdLife International 2004). The variability in the importance of the farmland scenario between species is probably related to differences in the use of the cropped areas. For instance, in Catalonia the common linnet occurs in a wide variety of habitats (Borràs et al. 2004) and therefore colonisers may not necessarily come only from the cropped areas, whereas the corn bunting is strongly dependent on this habitat type (Estrada and Orta 2004).

Regional variability in the species response to fire

Our results stress the importance of including the regional factor in order to explain the variability in the species colonisation patterns. One of the main reasons behind this result is likely to be the influence in the colonisation process of factors with a clear spatial component, such as dispersal limitations (Brotons et al. 2005) and historical factors (Kiss et al. 2004). For instance, in the Northeast region the presence of the studied species is mainly restricted to the most northern areas of the *Cap Creus* (see species distribution at Estrada et al. 2004). These areas have been historically maintained by the occurrence of wildfires (Díaz-Delgado et al. 2004a). This fact, together with the strong dispersal limitations of these species (Brotons et al. 2005) may explain the positive relation found between the fire scenario (mainly those wildfires occurring in the 80 s) and the postfire occurrence of some of the studied species. At the same time it is interesting to pinpoint the general negative effect of the other studied open-habitat types on species postfire colonisation in this region. These results suggest that the importance of biological processes and connectivity patterns on current species dynamics might depend on the particular location where they occur and on their interactions with other local factors not explicitly considered in this analysis.

Limitations and conclusions

This study supports the controversial point of view that, at least in the Northwest Mediterranean, wildfires are a key element in the conservation of some threatened bird

species. We have shown that wildfires generate adequate habitat for early-successional, open-habitat birds and that they may act as sources of immigrants for the new suitable habitat patches appearing in the landscape, highlighting the importance of recent fire regime to species conservation (Blondel and Aronson 1999; Brotons et al. 2008). Together with farmland areas and non-burnt shrubland areas, fires contribute to explain current post-fire colonisations by connectivity patterns. However, we recognize that our results on the probability of species colonisation are dependent on the description of the landscape scenarios and on the dispersal distance used. For instance, our approach makes assumptions about the minimum amount of suitable habitat a species population was considered sufficient to provide immigrants. This fact may have overestimated the importance of certain nodes and at the same time may have underestimated the importance as sources of immigrants of smaller habitat patches. A better understanding of how these habitat types function as sources of colonisers of these species is needed. Finally, not all studied species may match to the reference of a median dispersal distance of 12 km here used. Although we assume that the error of using the same dispersal distance would be low for species having similar functional role, this remains untested and further knowledge in the patterns of dispersal of these disturbance-sensitive species would be of great interest to further refine our findings in this study. Despite these limitations we still think that the results shown in the present paper are valuable to highlight the main processes constraining colonisation process at large scales and to provide novel insights into the current interactions between landscape and bird species dynamics in Mediterranean areas.

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References

- Alderman J, McCollin D, Hinsley SA, Bellamy PE, Picton P, Crockett R (2005) Modelling the effects of dispersal and landscape configuration on population distribution and viability in fragmented habitat. *Landscape Ecol* 20: 857–870
- Aymerich P, Santandreu J (2004) Trobat *Anthus campestris*. In: Estrada J, Pedrocchi V, Brotons L, Herrando S (eds) Catalan breeding bird atlas (1999–2002). Lynx, Barcelona
- Bibby CJ, Burgess ND, Hill DA (2000) Bird census techniques, 2nd edn. Academic Press, London
- BirdLife International (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife conservation series no. 12. BirdLife International, Cambridge
- Blondel J, Aronson J (1999) Biology and wildlife of the Mediterranean region. Oxford University Press, Oxford
- Borràs A, Senar JC, Cabrera J, Cabrera A (2004) Passerell comú *Carduelis cannabina*. In: Estrada J, Pedrocchi V, Brotons L, Herrando S (eds) Catalan breeding bird atlas (1999–2002). Lynx, Barcelona
- Bouma J, Varallyay G, Batjes NH (1998) Principal land use changes anticipated in Europe. *Agric Ecosyst Environ* 67:103–119
- Brotons L, Mañosa S, Estrada J (2004) Modelling the effects of irrigation schemes on the distribution of steppe birds in Mediterranean farmland. *Biodivers Conserv* 13: 1039–1058
- Brotons L, Pons P, Herrando S (2005) Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *J Biogeogr* 32:789–798
- Brotons L, Herrando S, Pons P (2008) Wildfires and the expansion of threatened farmland birds: the ortolan bunting, *Emberiza hortulana*, in Mediterranean landscapes. *J Appl Ecol* 45:1059–1066
- Burriel JA, Gracia C, Ibáñez JJ, Mata T, Vayreda J (2000–2004) Inventari Ecològic i Forestal de Catalunya (IEFC). CREAF, Bellaterra
- Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. *Trends Ecol Evol* 23:104–112
- Dale S, Lunde A, Steifetten Ø (2005) Longer breeding dispersal than natal dispersal in the ortolan bunting. *Behav Ecol* 16:20–24
- Dambrine E, Dupouey J-L, Laüt L, Humbert L, Thion M, Beaufils T, Richard H (2007) Present forest biodiversity patterns in France related to former roman agriculture. *Ecology* 88:1430–1439
- de Blois S, Domon G, Bouchard A (2001) Environmental, historical, and contextual determinants of vegetation cover: a landscape perspective. *Landscape Ecol* 16:421–436
- DGMN (Direcció General del Medi Natural) (1994) Pla General de Política Forestal. DARP: Departament d'Agricultura, Ramaderia i Pesca, Barcelona
- Díaz-Delgado R, Pons X (2001) Spatial patterns of forest fires in Catalonia (NE Spain) along the period 1975–1995. Analysis of vegetation recovery after fire. *For Ecol Manag* 147:67–74
- Díaz-Delgado R, Lloret F, Pons X (2004a) Spatial patterns of fire occurrence in Catalonia, NE, Spain. *Landscape Ecol* 13:731–745
- Díaz-Delgado R, Lloret F, Pons X (2004b) Statistical analysis of fire frequency models for Catalonia (NE Spain, 1975–1998) based on fire scar maps from Landsat MSS data. *Int J Wildland Fire* 13:89–99

- Donald PF, Green RE, Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc R Soc Lond B Biol Sci* 268:25–29
- Dupouey JL, Dambrine E, Laffite JD, Moares C (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83:2978–2984
- Estrada J, Orta J (2004) Cruixidell *Emberiza calandra*. In: Estrada J, Pedrocchi V, Brotons L, Herrando S (eds) Catalan breeding bird atlas (1999–2002). Lynx, Barcelona
- Estrada J, Pedrocchi V, Brotons L, Herrando S (2004) Atlas dels ocells nidificants de Catalunya (1999–2002). Lynx, ICO (Institut Català d'Ornitologia), Barcelona
- Farina A (1997) Landscape structure and breeding bird distribution in a sub-Mediterranean agro-ecosystem. *Landscape Ecol* 12:365–378
- Hanes TL (1971) Succession after fire in the chaparral of southern California. *Ecol Monogr* 41:27–52
- Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford
- Harding JS, Benfield EF, Bolstad PV, Helfman GS, Jones EBD (1998) Stream biodiversity: the ghost of land use past. *Proc Natl Acad Sci USA* 95:14843–14847
- Heckenberger MJ, Kuikuro A, Kuikuro UT, Russell JC, Schmidt M, Fausto C, Franchetto B (2003) Amazonia 1492: pristine forest or cultural parkland? *Science* 301:1710–1714
- Herrando S, Brotons L, del Amo R, Llacuna S (2002) Bird community succession after fire in a dry mediterranean shrubland. *Ardea* 90:303–310
- Jacquet K, Prodon R (2009) Measuring the postfire resilience of a bird–vegetation system: a 28-year study in a Mediterranean oak woodland. *Oecologia* 161:801–811
- Kiss L, Magnin F, Torre F (2004) The role of landscape history and persistent biogeographical patterns in shaping the responses of Mediterranean land snail communities to recent fire disturbances. *J Biogeogr* 31:145–157
- Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Rodà F, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. *Trends Ecol Evol* 24:564–571
- Lindborg R, Eriksson O (2004) Historical landscape connectivity affects present plant species diversity. *Ecology* 85:1840–1845
- Lloret F (1998) Fire, canopy cover and seedling dynamics in Mediterranean shrubland of northeastern Spain. *J Veg Sci* 9:417–430
- Lloret F, Calvo E, Pons X, Diaz-Delgado R (2002) Wildfires and landscape patterns in the Eastern Iberian Peninsula. *Landscape Ecol* 17:745–759
- Mañosa S, Estrada J, Folch A, Bonfil J, González-Prat F, Orta J (1996) Bird-habitat relationships in the Catalan steppes. In: Fernández Gutiérrez J, Sanz-Zuasti J (eds) Conservación de las Aves Esteparias y sus Hábitats. Junta de Castilla y León, Valladolid, pp 153–161
- Moloney KA, Levin SA (1996) The effects of disturbance architecture on landscape-level population dynamics. *Ecology* 77:375–394
- Moreira F, Russo S (2007) Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. *Landscape Ecol* 22:1461–1476
- Moreira F, Rego FC, Ferreira PG (2001) Temporal (1958–1995) pattern of change in a cultural landscape of northwestern Portugal: implications for fire occurrence. *Landscape Ecol* 16:557–567
- Moreno JM, Oechel WC (1994) The role of fire in Mediterranean-type ecosystems. Springer, New York, p 201
- Muntaner J, Ferrer X, Martínez-Vilalta A (1984) Atlas dels ocells nidificants de Catalunya I Andorra. Ketres, Barcelona
- Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. *J Anim Ecol* 67:518–536
- Pausas JG (2004) Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Clim Chang* 63:337–350
- Piñol J, Terradas J, Lloret F (1998) Climate warming, wildfire hazard and wildfire occurrence in coastal Eastern Spain. *Clim Chang* 38:345–357
- Pons P, Bas JM (2005) Open-habitat birds in recently burned areas: the role of the fire extent and species' habitat breadth. *Ardeola* 52:119–131
- Pons P, Prodon R (1996) Short term temporal patterns in a Mediterranean shrubland bird community after wildfire. *Acta Oecol* 17:29–41
- Preiss E, Martin JL, Debussche M (1997) Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. *Landscape Ecol* 12:51–61
- Prodon R, Lebreton JD (1981) Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees. Analysis and modelling of the structure gradient. *Oikos* 37:21–38
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Russo D (2007) The effects of land abandonment on animal species in Europe: conservation and management implications. Integrated assessment of vulnerable ecosystems under global change in European Union. Project report. European Commission, Community Research, Sustainable Development, Global Change and Ecosystems
- Sanderson FJ, Donald PF, Burfield IJ (2005) Farmland birds in Europe: from policy change to population decline and back again. In: Bota G, Morales MB, Mañosa S, Camprodon J (eds) Ecology and conservation of steppe-land birds. Lynx Edicions & Centre Tecnològic Forestal de Catalunya, Barcelona, pp 211–236
- Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landsc Urban Plan* 83:91–103
- Saura S, Rubio L (2010) A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography* 33:523–537
- Saura S, Torné J (2009) Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. *Environ Model Softw* 24:135–139
- Sirami C, Brotons L, Martin JL (2007) Vegetation and songbird response to land abandonment: from landscape to census plot. *Divers Distrib* 13:42–52

- Sirami C, Brotons L, Burfield I, Fonderflick J, Martin JL (2008) Is land abandonment having an effect on biodiversity? A meta-analytical approach to bird distribution changes in the north-west Mediterranean. *Biol Conserv* 141:450–459
- Sirami C, Nespoulous A, Cheylan JP, Marty P, Hvenegaard GT, Martin J-L (2010) Long-term anthropogenic and ecological dynamics of a Mediterranean landscape: impacts on multiple taxa. *Landsc Urban Plan* 96:214–223
- Urban D, Keitt T (2001) Landscape connectivity: a graph theoretic perspective. *Ecology* 82:1205–1218
- Vallecillo S, Brotons L, Herrando S (2008) Assessing the response of open-habitat bird species to landscape changes in Mediterranean mosaics. *Biodivers Conserv* 17:103–119
- Vallecillo S, Brotons L, Thuiller W (2009) Dangers of predicting bird species distributions in response to land-cover changes. *Ecol Appl* 19:538–549
- Venables WN, Ripley BD (2002) *Modern applied statistics with S*, 4th edn. Springer, New York
- Villard M-A, Trzcinski MK, Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conserv Biol* 13:774–783
- Zozaya EL, Brotons L, Herrando S, Pons P, Rost J, Clavero M (2010) Monitoring spatial and temporal dynamics of bird communities in Mediterranean landscapes affected by large wildfires. *Ardeola* 57:33–50
- Zozaya EL, Brotons L, Vallecillo S (2011) Bird community responses to vegetation heterogeneity following non-direct regeneration of Mediterranean forests after fire. *Ardea* 99:73–84
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York