

Wildfires and the expansion of threatened farmland birds: the ortolan bunting *Emberiza hortulana* in Mediterranean landscapes

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Summary

1. It has been argued that wildfires are one of the major agents involved in landscape transformation in many European regions and their impact is expected to increase in the near future. Despite the recognized impact of fire on wildlife at a local scale, we lack information on the species responses to fire at larger spatial scales.

2. In this study, we used the ortolan bunting *Emberiza hortulana* to evaluate the potential effects of wildfires on open-habitat species distribution. In contrast to most European countries, this farmland species has experienced a consistent range expansion during the last decades in Catalonia (northeast Iberian peninsula). Distribution data of the species collected at different time periods allowed us to test the role of fires in determining range expansions at a regional scale, and to evaluate the importance of dispersal constraints on distribution changes.

3. Analyses of distribution data from 1975–1983 and 1999–2002 showed a consistent expansion of the ortolan bunting in Catalonia. After correcting for differences in sampling effort, changes in distribution showed a strong spatial pattern with colonization and stability, but not local extinction, being clumped in space. Patterns of change were also strongly and significantly associated with the amount of shrubland burnt between the two time periods, since areas that experienced a larger impact of fires in terms of burnt area showed a much higher probability of maintaining species presence or of being colonized. Colonization events appeared to be more likely in areas affected by fire especially when surrounding areas had already been colonized by the species.

4. *Synthesis and applications.* Overall, our results support the hypothesis that wildfires, especially those affecting open woodlands or shrubby areas, play a critical role in the ecology of the ortolan bunting and have contributed to the recent expansion of the species in Catalonia. Furthermore, we have shown that colonization appears to be limited, not only by the availability of new burnt habitat but also by specific dispersal constraints. We suggest that, for several European threatened species associated with open habitats, burnt areas may partially compensate for the widespread loss and deterioration of farmland habitat, opening new management opportunities for their conservation.

Key-words: atlas data, colonization, dispersal, disturbance, farmland birds, generalized linear models, local extinction

Introduction

Large-scale environmental change, directly or indirectly related to human activity, has important effects on biodiversity (Vitousek *et al.* 1997; Sax & Gaines 2003). Rapid changes in agricultural practices, including intensification (Brotons,

Mañosa & Estrada 2004), large-scale afforestation (Diaz *et al.* 1998) and pollution (Fuller *et al.* 1995) are currently the main threats for many species in Europe (Tucker & Evans 1997). Open-habitat birds have become a paradigm of the impacts of these changes, thanks to their well-surveyed populations and the reported evidence linking both phenomena (Fuller *et al.* 1995; Gregory & Baillie 1998; Donald, Green & Heath 2001b). The ortolan bunting *Emberiza hortulana* (L.) is a

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good example of a species suffering large-scale declines across Europe. Its population has decreased in 21 out of 36 countries between 1990 and 2000, and no increase has been reported in any country for the same period (BirdLife International 2004). Some countries such as Finland, report as much as 72% population loss in the last 20 years (Vepsäläinen *et al.* 2005). This has led to the classification of the species as SPEC 2 (i.e. global populations concentrated in Europe and unfavourable conservation status) and its European conservation status as 'Depleted' (BirdLife International 2004). As has been described for a number of farmland-related species (Fuller *et al.* 1995; Donald *et al.* 2001a; Kujawa 2002), decreases in the ortolan bunting populations appear to be related to general habitat loss and degradation as a consequence of farming intensification and homogenization of agricultural landscapes (Dale 2001; Fonderflick, Thevenot & Guillaume 2005; Vepsäläinen *et al.* 2005). Although impacts on the wintering grounds may potentially contribute to declining trends, available data suggest these factors to be of secondary importance (Dale 2001).

In sharp contrast with the overall European trends, a recent breeding bird atlas survey conducted in Catalonia (northeastern Iberian Peninsula) offers a new regional perspective of temporal changes in the species distribution. Here, the ortolan bunting has almost doubled its breeding range in the last 20 years and, consequently, although its population in Catalonia is estimated at about 15 000 pairs, its regional International Union for the Conservation of Nature and Natural Resources conservation status is 'Least Concern' (Estrada *et al.* 2004). Whereas the main trends in agricultural practice (i.e. intensification in lowlands and abandonment in the less productive mountainous areas) appear to be similar to those prevailing in other European regions (Brotons *et al.* 2004; Sirami, Brotons & Martin 2007), wildfires have recently been hypothesized as a potential cause of the expansion of the species in Catalonia (Pons 2004).

Some evidence are available on the potential of non-farmland habitats as alternative habitat for farmland birds (Fuller, Hinsley & Swetnam 2004). Other open-habitat species of conservation concern at the European level such as red-legged partridge *Alectoris rufa*, thekla lark *Galerida theklae*, tawny pipit *Anthus campestris* or some wheatears *Oenanthe hispanica* and *O. leucura* are known to benefit from the changes in vegetation structure induced by wildfires (Tucker & Evans 1997). However, the ortolan bunting is the species that has shown the greatest expansion in Catalonia during the last 20 years (Estrada *et al.* 2004). It has been suggested that it may be more adaptable to fire-related habitat than other species with similar habitat requirements (Pons 2004). Although the ortolan bunting may be found in several habitat types in Catalonia, from sea level to alpine meadows (Estrada *et al.* 2004), previous work has indicated that in Catalonia the species makes extensive use of recently burnt areas in relatively high densities (Pons & Prodon 1996; Herrando *et al.* 2002; Pons & Bas 2005). The use of recently burnt areas has also been reported from other European countries such as Switzerland and Norway (Dale & Olsen 2002; Revaz *et al.*

2005). The ortolan bunting tends to disappear from most habitats as vegetation recovers (Sirami *et al.* 2007) and, therefore, the impact of fire on the distribution of the species is likely to depend on the frequency, severity and total area affected by this disturbance. However, at present, the role of fire dynamics on the large-scale distribution and population trends of open-habitat species such as the ortolan bunting remains largely unknown.

In this study, we aimed to identify the role of fire in the current distribution of the ortolan bunting in Catalonia and then explore the factors that have contributed to its expansion and persistence at the landscape scale. For fire-associated habitats to be judged to be of value to the ortolan bunting, two conditions have to be met: (i) new burnt habitats should be colonized by the species, and (ii) the species should be able to persist in colonized habitats a number of years after the perturbation event. We analysed colonization patterns of the species for two periods 20 years apart by means of data from the recently published *Catalan Breeding Bird Atlas 1999–2002* (Estrada *et al.* 2004). Along with information on changes in the bird's breeding range, we used data on fire occurrences (1983–1999) to investigate the role of wildfires in determining long-term changes in the distribution of the species. Since colonization of new, potentially suitable habitats, such as those deriving from fire disturbance, may be constrained by the species' dispersal capability, we addressed the hypothesis that distribution is also shaped by such limitations by explicitly incorporating the spatial structure of persistence and colonization pattern in the analyses.

Methods

STUDY AREA

The study was conducted in Catalonia, a region dominated by a Mediterranean climate located in the northeastern corner of the Iberian Peninsula (Fig. 1). Despite its small size (about 32 000 km²), it is remarkably heterogeneous due to sharp climatic and geological gradients, including a range of landscapes from alpine habitats to coastal marshes, and from evergreen forests to steppes and agricultural mosaics.

We use the word wildland throughout the text to refer to those areas covered either by woodland or forests (forested wildland) or shrublands (non-forested wildland, tree cover < 20%), which represent the majority of natural habitats in Catalonia; wetlands, grasslands and rocky outcrops are much less represented. According to the land use map of Catalonia (Viñas & Baulies 1995), the total wildland area in the region is more than 1.95 million ha (73% forests and 27% shrublands). Shrublands have a wide and diverse species composition, but they mainly comprise evergreen plants (Folch 1981). According to the First Forest Inventory of Catalonia (Gracia *et al.* 2003), scots pine, *Pinus sylvestris*, forest covers 20% of the woodland, a percentage similar to that of Aleppo pine, *Pinus halepensis*, forest; next, in order of importance, are holm oak, *Quercus ilex* (16.6%), black pine, *Pinus nigra* (12.5%), cork oak, *Quercus suber* (5.5%), downy oak, *Quercus humilis* (4%) and other more scarce species such as stone pine, *Pinus pinea*; fir, *Abies alba*; chestnut, *Castanea sativa*; beech, *Fagus sylvatica*; maritime pine, *Pinus pinaster*; and lusitanian oak, *Quercus faginea*.

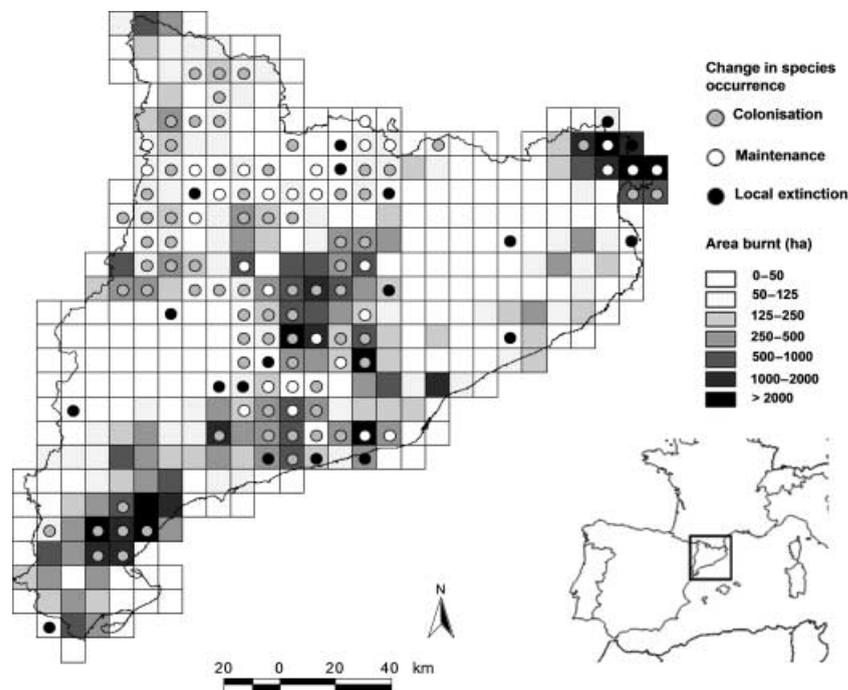


Fig. 1. Distribution of the ortolan bunting from the *Catalan Breeding Bird Atlas* in two time periods: 1975–1983 and 1999–2002. Circles represent changes in the species' breeding status between the first and the second atlases. Grey scale in the squares of the grid shows the total area burnt (ha) between 1983 and 1999 per 10×10 km UTM square.

LARGE-SCALE DISTRIBUTION DATA

In our assessment of the factors behind changes in distribution of the ortolan bunting, we used species-occurrence data derived from the *Catalan Breeding Bird Atlas*. The atlas data consist of large-scale surveys covering the entire extent of Catalonia in two different periods: 1975–1983 (Atlas1) and 1999–2002 (Atlas2). A total of 385 10×10 km Universal Transverse Mercator (UTM) squares were surveyed during the atlas field work in each of the different time periods (Fig. 1). The aim of the survey was to detect the highest number of breeding species. From March to July inclusive, observers were asked to gather evidence of bird species breeding in all representative habitats within their kilometre square. Squares were thereafter categorized according to the recorded changes in species occurrence as: colonized (present in Atlas2 but not in Atlas1), locally extinct (present in Atlas1 but not in Atlas2), maintained (present in both periods) and absent (absent in both periods).

For a particular species, the changes in distribution at a regional scale can be estimated by means of an analysis of the changes occurred in every UTM 10×10 km square (Fuller *et al.* 1995; Donald & Fuller 1998). However, this approach does not distinguish between changes in distribution due to temporal variation in sampling effort, which may mask real distribution changes (Donald & Fuller 1998). To avoid this bias, we used estimates of effective sampling effort as co-variables in further analyses of changes in species' distribution between atlases. Sampling effort was calculated by means of timed censuses conducted in a sample of UTM 1×1 km squares located within each of the UTM 10×10 km squares. Species-time accumulation curves were drawn from these data and used to estimate the effective surveying effort required for any particular value of species richness in each of the two atlases (see Estrada *et al.* 2004 for further description). Analyses of distributional changes were only carried out on 80% of squares ($N = 309$) from which changes in sampling effort could be obtained. The 20% of squares excluded from the analysis have a minor importance in terms of the

geographic representation of Catalonia since they corresponded to squares with less than 50% of Catalan territory (located either on political borders or on the coast).

Species distributions and their dynamics usually show a strong spatial component originating from a variety of ecological processes occurring at different spatial scales (i.e. spatial autocorrelation; Selmi & Boulinier 2001; Diniz-Filho, Bini & Hawkins 2003). In our study, we explicitly included the spatial structure of the species' distribution and the colonization process in the modelling approach in order to account for spatial processes related to dispersal in the recorded changes in the distribution of the ortolan bunting (Brotons, Pons & Herrando 2005; Gimona & Brewer 2006). We summarized, for a given UTM 10×10 km square, information about species occurrence or change in surrounding squares by means of contagion variables (Augustin, Muggleston & Buckland 1996). Contagion variables were calculated in two different methods: by using only the eight surrounding squares (A); and by using information on surrounding squares located up to 40 km away and weighting their contribution to the final contagion value exponentially in proportion to their distance (B). We generated different contagion variables according to the type of change in breeding status occurring in each square: squares occupied in Atlas1, colonized squares and a third contagion variables accounting for stable squares and squares for which local extinction had been recorded.

IMPACT OF FIRE IN THE REGION

In the Mediterranean Basin, fire is a common disturbance (Mouillot & Field 2005). Fires have had a strong impact in Catalan landscapes and the size of burnt areas have increased in recent years, most probably due to fuel accumulation and increase in the number of days with high temperature and low air humidity (Piñol, Terradas & Lloret 1998). From a recent study on fire dynamics in Catalonia (Diaz-Delgado, Lloret & Pons 2004), it was established that approximately 240 000 ha were burnt between 1975 and 1998 (i.e.

approximately 13% of total wildland area). Large fires have played an important role, with 10% of fires accounting for 86% of the total burnt wildland area, and fires larger than 20 km² (6%) representing 61% of this total area. The analysis gives a natural fire rotation period of about 133 years in agreement with similar studies from other Mediterranean-type ecosystems (Diaz-Delgado *et al.* 2004).

We collected information on the extent of wildfires for 1983–1999 (the period between the two bird atlases) from government statistics at the municipal level (Catalan Department of Housing and Environment, http://mediambient.gencat.net/cat/el_medi/incendis/). We aggregated the total surface of burnt area accumulated for all municipalities within a given 10 × 10 km UTM square. Where a municipality extended beyond one UTM square and fire had been recorded during the study period, we allocated burnt surface to each 10 × 10 km square according to the amount of shrubland present in the municipality as estimated by the land use map of Catalonia in 1998 (Viñas & Baulies 1995). Since, the wildfire data base provides information on the total area burnt per municipality but also differentiates between the amount of tree-covered burnt area (burnt forested wildland) and the amount of tree-less, shrubland burnt area (non-forested wildland), for each square we obtained two different statistics describing fire impact during the study period: the area of burnt forested wildland and the area of burnt non-forested wildland.

STATISTICAL ANALYSES

We used multinomial error distribution generalized linear models (McCullagh & Nelder 1989) to model the historical trajectories of the ortolan bunting occurrence between the two atlas periods (absence, stability, local extinction and colonization) as a function of different explanatory variables. We used a hierarchical modelling approach to progressively assess the role of these variables in four different steps (Herrando & Brotons 2002a). We assessed the role of new variables at each step by means of change in model deviance (McCullagh & Nelder 1989). Significant variables at each step were included in later steps.

Step 1. As changes in bird distribution in each 10 × 10 km UTM square may be strongly influenced by changes in sampling effort between study periods, we included variation of effective sampling effort between the two atlases (log transformed) as the first controlling variable in the models.

Step 2. Spatial processes are likely to underline changes in distribution between two time periods via ecological processes such as dispersal constraints (Selmi & Boulinier 2001). Therefore, we included different spatial variables (contagion autocovariates) in the models summarizing information on the species occurrence in the vicinity of a given square. More explicitly, this allowed us to test two hypotheses: (i) colonization may be more likely in the area immediately surrounding the original distribution (squares where the species was present in Atlas1), and (ii) colonization may be more likely in the area surrounding a colonized area (squares where the species was absent in Atlas1 and was present in Atlas2). We included two contagion variables to test these two hypotheses at this step: number of occupied squares in Atlas1 around a given square for hypothesis (i), and number of squares colonized around a given square for hypothesis (ii). Finally, we explored the possible spatial patterns on local extinctions and stability. Local extinctions and stable squares would also be expected to be spatially autocorrelated if nearby populations help maintain viable populations. We included a third contagion variable accounting for the mean number of local extinctions and stable squares occurring between the time periods covered by Atlas1 and Atlas2.

Step 3. We tested whether burnt area in each 10 × 10 UTM square in the period between the two atlases explained the distributional change in this period. We used the amount of burnt area between Atlas1 and Atlas2 (non-forested and forested wildland) as explanatory variables in the model. In this step, we also assessed the availability of total shrubland cover (including habitats unrelated to fires) in order to disentangle the role of this variable from the effects of fire originated shrubland. These data were obtained from a 1998 land cover map derived from satellite imagery, and included forest (tree cover > 20%) and shrubland as main categories of semi-natural vegetation potentially affected by fire (see methods in Viñas & Baulies 1995).

Step 4. Since we expect colonization processes to be favoured in cases in which new suitable habitats appear near a potential colonizer source (Brotons *et al.* 2005), we also assessed the interaction between the amount of burnt areas in each square and the presence of potential colonizer sources in the vicinity (i.e. contagion variables).

To assess the effect of the spatial extent over which the analyses were conducted, we ran the modelling process above using different sets of 10 × 10 km UTM squares. We used all squares available in Catalonia (Model 1) but also a subsample containing only those squares occupied by the species either in Atlas1 or in Atlas2, or in both (Model 2). Both analyses were repeated for the two different types of contagion variable calculations. Since results were similar irrespective of the method used to calculate contagion variables, we only show the results using contagion variables calculated using method B (see above). Finally, Moran's I autocorrelograms were used to assess spatial autocorrelation patterns in environmental variables and model residuals.

Results

CHANGES IN BIRD DISTRIBUTION PATTERNS AND FIRE

The number of 10 × 10 UTM squares occupied by breeding ortolan bunting increased from 50 during the period 1975–1983 to 109 in 1999–2002. After controlling for variation in sampling effort (modelling step 1, Table 1), there was an 88% increase concentrated in large areas in central, northwest and southwest Catalonia (Fig. 1).

Changes in the distribution of the ortolan bunting between the two study periods had a strong spatial component (modelling step 2, Table 1). In particular, colonization events appeared to be clumped in space, and showed significant spatial autocorrelation up to distances of 50 km (Figs. 1 and 2). The colonization of new squares in Atlas2 was strongly associated with the occurrence of the species in neighbouring squares in Atlas1 and the occurrence of colonization events in neighbouring squares (Table 1). The occurrence of the species around any given square (being its presence in Atlas1 or a newly colonized square) was a good predictor of the probability of colonization. These two variables proved to be significant into the models, both when all data (Model 1) and when only the subset of squares occupied either in Atlas1 or Atlas2 were analysed (Model 2, Table 1).

After accounting for effort and spatial contagion variables, we found that the amount of burnt area within a 10 × 10 km UTM square had a consistent significant effect on the pattern of change between the two atlases (modelling step 3, Table 1).

Table 1. Analyses of the factors behind changes in ortolan bunting distribution between the two atlas periods. We performed generalized linear modelling (multinomial distribution) using distributional change as dependent variable with four categories: local extinction, stability, colonization and absence. Best hierarchical models are shown for different extents of species distribution: Model 1 included all squares in Catalonia for which estimates of variation in sampling effort were available (four different categories, $n = 309$). Model 2 included only squares where the species was present either in Atlas1 or in Atlas2 (i.e. three categories thus excluding 'absences', $n = 104$). Only best models including significant variables (or those included in significant interactions) at each step are shown. Variables: Δ Effort (change in sampling effort between the two atlas periods), $Atlas1_c$ and Col_c (contagion variables summarising number of presence squares in Atlas1 and number of colonized neighbouring squares) and wildland area (ha) burnt between the two atlas periods ($Burnt_n$, non-forested burnt wildland and $Burnt_f$, forested burnt wildland)

	Variables	Model 1		Variables	Model 2	
		Change in d.f.	Change in model deviance (χ^2)		Change in d.f.	Change in model deviance (χ^2)
Null model		924	583.5		206	187.5
Step 1	Δ Effort*	3	9.8	Δ Effort**	2	11.2
Step 2	$Atlas1_c$ *** Col_c **	6	141.5	$Atlas1_c$ * Col_c *	2	11.5
Step 3	$Burnt_n$ *** $Burnt_f$ (N.S.)	6	22.7	$Burnt_n$ ** $Burnt_f$ (N.S.)	4	11.2
Step 4	$Atlas1_c \times Burnt_n$ ** $Atlas1_c \times Burnt_f$ **	6	14.5	$Col_c \times Burnt_n$ *** $Col_c \times Burnt_f$ ***	4	18

* < 0.05 , ** < 0.01 , *** < 0.001 .

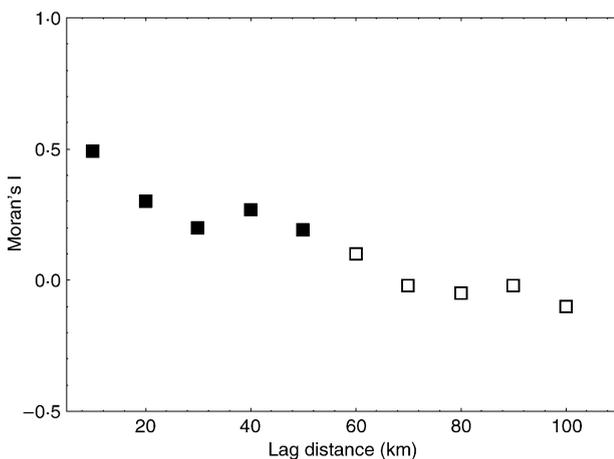


Fig. 2. Moran's I spatial correlogram for colonization pattern of the ortolan bunting between the two atlases (1975–1983 and 1999–2002). Significant ($P < 0.05$) Moran's I spatial correlation coefficients are shown as black squares.

Squares with a larger proportion of burnt area had a much higher probability of being colonized or remaining occupied by the ortolan bunting during the study period than squares subject to fewer fires (Figs. 3 and 4). However, this relationship tended to be strongest when considering the area of burnt non-forested wildland, rather than forest or total burnt area (Table 1). Again the spatial extent over which the analyses were conducted had little effect on the results both when all data were analysed (Model 1) and when only the subset of

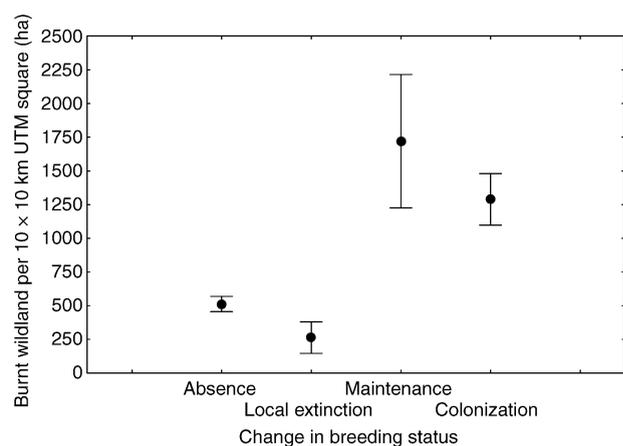


Fig. 3. Mean burnt surface of wildland per 10×10 km UTM square according to the type of documented change in species breeding status between the two atlases (1975–1983 and 1999–2002). Bars represent standard errors.

squares occupied either in Atlas1 or Atlas2 was used (Model 2, Table 1). Total area of shrubland in each square (whether originated by fire or not) was not a good predictor of change (Model 1, $\chi^2 = 3.34$, d.f. = 3, Model 2, $\chi^2 = 3.71$, d.f. = 2).

Finally, we found that the pattern of change in ortolan bunting distribution was significantly associated with the interaction between burnt wildland and contagion variables (modelling step 4). In particular, for Model 1 (i.e. all squares analysed), higher colonization probability was associated

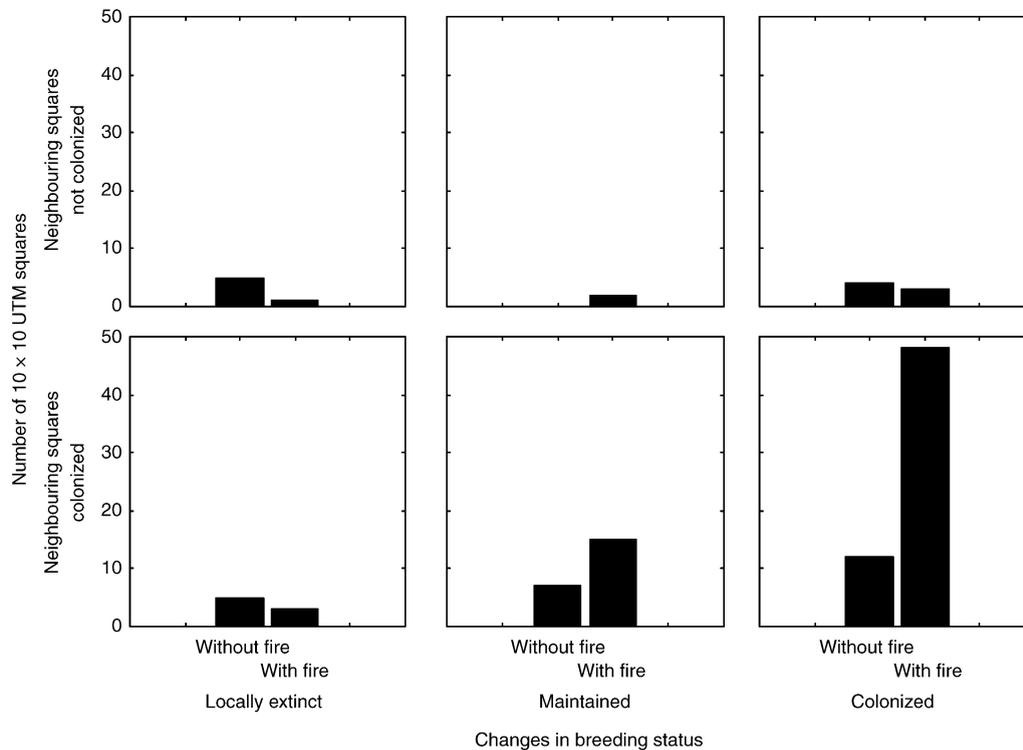


Fig. 4. Distribution of documented changes in species breeding status in 10×10 km UTM squares between the two atlas periods (1975–1983 and 1999–2002) according to the impact of wildfires (without fire: less than 100 ha of the square affected; with fire: more than 100 ha affected) and whether or not between the two atlas periods the species had colonized at least one neighbouring square.

with an occurrence of neighbouring occupied squares in Atlas1 in areas affected by wildfires, either forested or non-forested wildland (Table 1). For Model 2 (i.e. including the subset of squares occupied either in Atlas1 or Atlas2), colonization was proportionally more likely in burnt areas (either burnt forested or burnt non-forested wildland) with neighbouring colonization events having taken place between the two atlas periods (Table 1, Fig. 4).

Discussion

Our results support the hypothesis that fire plays a critical role in the distribution dynamics of an open-habitat species such as the ortolan bunting in Mediterranean areas. We have established, for the first time, a direct link between the impact of fire and the expansion at the regional scale of a European threatened bird species. After correction for changes in sampling effort, colonization–extinction patterns for the species in Catalonia were significantly related to the occurrence of wildfires at the landscape scale. Identifying the causes behind the association of wildfires and range expansions of the ortolan bunting in Catalonia is out of the scope of our correlative approach. However, the available information suggests that this link is most probably related to the changes in vegetation structure induced by fires (Pons & Prodon 1996). It is not known whether changes in vegetation structure are associated with increases in food availability or lower predation rates for the species in burnt areas, so future studies should

concentrate on gathering information from individuals within focal populations. Burnt areas may complement other habitats by providing resources such as nest sites that are not available elsewhere. There is evidence from the Norwegian ortolan bunting population that burnt areas improve the colonization potential of farmland habitat by providing additional resources, i.e. males nesting in burnt habitat use adjacent farmland as foraging grounds (Dale & Olsen, 2002).

The expansion of the range of the ortolan bunting in Catalonia is clearly a complex process. First, the colonization of new areas occurred most frequently near to previously occupied areas. This spatial pattern was also found for other open-habitat species in Catalonia (Brotons *et al.* 2005). Second, colonization and the subsequent stability of the species is greatest in areas most affected by wildfires. Overall, colonization was most likely in burnt areas near to existing or expanding ortolan bunting populations. These results suggest that the colonization of new areas by this bird is driven by two main factors: the availability of new suitable habitat patches (i.e. those created by fires), and the constraints imposed by its dispersal ability limiting its expansion to nearby sites.

Recent studies suggest that the ortolan bunting can undertake long-distance dispersal in both the breeding and the post-fledging period, with recorded distances of up to 45 km (Dale, Lunde & Steifetten 2005). This matches the distance within which our colonization data showed spatial correlation, suggesting that this value may be related to the limits of dispersal for this bunting. For a species that relies on the availability of

patchy and dynamic habitats (such as burnt areas), dispersal capability may be crucial in locating suitable areas in which to establish breeding territories and is a key factor in the overall dynamics of ortolan bunting distribution. Under favourable conditions, colonization proceeds mainly by diffusion limited by dispersal constraints; long-distance dispersal may lead to colonization of new habitats far from the main breeding areas (Brotons *et al.* 2005). In this context, large fires may play a critical role in seeding new populations by creating large favourable habitat patches suitable for colonization (Hanski 1999). Further studies should concentrate on the process of colonization and the constraint that size and inter-patch distances impose on species' dispersal within fire-dominated landscapes.

New burnt areas offer suitable habitat for open-habitat species such as the ortolan bunting. In local studies, such as those conducted in southern France, it appears as a pioneer species after fire (Pons & Prodon 1996); this seems likely to be a general pattern in the western Mediterranean Basin where the ortolan bunting occurred in nine out of 21 burnt areas studied by Pons & Bas (2005). In Norway and Switzerland, the species uses burnt patches for breeding and uses nearby agricultural habitats for foraging (Dale & Olsen 2002; Revaz *et al.* 2005). The fact that burnt area rather than total shrub area is a significant predictor of distribution change for the ortolan bunting in Catalonia suggests that impact of fire per se is the critical process in the creation of new habitat suitable for the species.

Indeed, the pattern of change in the distribution of the ortolan bunting in Catalonia was more strongly related to the amount of non-forested burnt wildland, which was previously covered by shrubland, rather than forest or total burnt area. These results suggest that burnt shrubland areas have a higher likelihood of being colonized than burnt forest. This may be because areas of burnt forest may be farther away from local populations (Brotons *et al.* 2005). In fact, when we included potential sources of colonization in our models (i.e. contagion variables), their interaction with the burnt forested wildland area appeared as a significant predictor of distribution change. Alternatively, our results also suggest that burnt forest is unsuitable for ortolan bunting immediately after fire due to the large amount of dead standing wood and tree branches. Although standing wood is usually removed by forest owners to be sold, in general burnt forest habitat may be less suitable than burnt shrubland habitat. Furthermore, forested areas tend to be associated with more productive sites (Thuiller *et al.* 2003), which may enhance vegetation recovery and reduce the time window in which open habitats are potentially available for colonization by the ortolan bunting. Overall, our results support the view that typical forest fires may not always generate optimal habitat for the species.

CONSERVATION IMPLICATIONS

The role of fire may be critical for many threatened species of European conservation concern (Moreira *et al.* 2001). Indeed, Pons & Bas (2005) showed that 17 out of 22 open-habitat bird

species using recently burnt areas in Iberia and southern France had an unfavourable conservation status in Europe, and that large burnt areas showed more diverse avian communities than small ones. Here we have shown for the first time at a large spatial scale that fires of thousands of hectares are able to drive large-scale range expansions of a species that is strongly declining elsewhere in Europe. Since fires are a prominent factor impacting landscapes across the Mediterranean Basin, we suggest that population status and trends of the ortolan bunting in this region should be carefully reassessed. The frequency of wildfire is likely to be important in the recovery of other species typical of open habitat areas that have significantly increased their distribution in Catalonia during the last 20 years (Estrada *et al.* 2004).

Moreover, the role of fire and the reported distribution dynamics of the ortolan bunting complement recent statements claiming that the widespread decline of the species in Europe may be linked to changes in migration and wintering areas (Bohning-Gaese & Bauer 1996; Sanderson *et al.* 2006) or to deterioration of farmland habitat quality (Donald *et al.* 2001b). While our results do not contradict any of these hypotheses, they clearly suggest that availability and quality of non-farmland habitat during the breeding season is potentially a major factor behind the dynamics of the species at large spatial scales (Fuller *et al.* 2004).

Some management recommendations may be derived from our findings that fire-related habitat is associated with the expansion of the ortolan bunting, opening a range of new opportunities for the conservation of this species that can probably be extended to other threatened open-habitat birds. First, areas affected by wildfires, especially when these are large (several hundreds of hectares, Pons & Bas 2005) and occur near to known populations of a target species, are likely to be colonized. These areas could be targeted for habitat management directed towards enhanced population persistence. In particular, by slowing down vegetation succession, the diversity and conservation status of open-habitat species will be enhanced, and fuel load will be reduced, thereby reducing the threat of large and catastrophic wildfires. Plant growth could be limited by increasing grazing through the reintroduction of large herbivores or livestock husbandry (Pulido & Díaz 1992). Another option is prescribed burning, now widely used elsewhere, as a management tool to prevent large-scale catastrophic wildfires (Hardy & Arno 1996). Prescribed burning usually has a relatively modest impact on bird communities (Petersen & Best 1987; Pons *et al.* 2003) but it may be of great utility in non-Mediterranean regions where fires are scarce and are known to benefit highly threatened populations of open-habitat birds (Dale & Olsen, 2002; Revaz *et al.* 2005). Future research efforts should concentrate on providing more specific guidelines on habitat management using fire to maximize biodiversity.

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