



# Colonization of dynamic Mediterranean landscapes: where do birds come from after fire?

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## ABSTRACT

**Aim** Two main mechanisms may explain post-disturbance species colonization patterns of early successional habitats such as those originated by wildfires. First, post-disturbance colonization is not limited by the dispersal ability of the species to reach the newly created open areas and secondly, colonization is limited by dispersal. Under the first hypothesis, we expect, at a regional scale, to find similar post-disturbance communities to develop on recently burned sites. However, colonization limited by dispersal will lead to strong between-site variations in species composition.

**Location** To test these hypotheses, we studied the post-fire colonization patterns of nine open-habitat bird species in eight distantly located wildfires in the north-eastern Iberian Peninsula.

**Methods** We censused post-fire bird composition by means of field transects and identified potential colonization sources from species–habitat suitability maps derived from atlas data.

**Results** Our results showed strong significant differences in post-fire species composition between burnt areas. Burnt areas located in areas with low probability of species presence before the fire event showed lower species occurrence and richness after the fire.

**Main conclusions** These results do not support the idea that early successional stages and open habitats have a homogeneous community structure at regional scales and suggest that dispersal is a key constraint determining bird colonization of post-fire habitats. Further attention should be paid to landscape heterogeneity as a key factor in determining population dynamics of open-habitat species in the light of current and future land use changes in Mediterranean regions.

## Keywords

Disturbance, heterogeneity, dispersal, bird distribution, landscape change.

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## INTRODUCTION

The role of disturbance in moulding the structure and function of biological systems is a major paradigm in ecology. Natural disturbances play a fundamental role in maintaining the heterogeneity of environmental conditions that organisms experience through space, time or both (Pickett *et al.*, 1989; Brawn *et al.*, 2001). By transforming landscapes, disturbances modify or create local conditions and make them suitable to a number of species. The species that occupy recently disturbed sites will depend on different factors such as site fidelity or

colonization ability that will allow species originally absent to immigrate to new habitats (Jenkins & Buikema, 1998; Pons, 1998; Lavorel *et al.*, 1999; Buddle *et al.*, 2000). Understanding the processes determining a species ability to colonize has been a major topic of island biogeography and metapopulation theory (MacArthur & Wilson, 1967; Hanski, 1999). These theories consider the dynamics of colonization and extinction as the main drivers of species distribution. The colonization of a new appearing habitat becomes a function of its area and of its effective isolation. The latter depends on both the distance to potential sources of colonization, and the dispersal

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1 capability of the colonizer. For pioneer species associated with dynamic, early successional habitats, it is commonly assumed that good dispersal capability allows them to easily colonize post-disturbance habitats, i.e. the 'colonizer syndrome' (Hutchinson, 1951; Baker & Stebbins, 1977). Theoretical models on the evolution of dispersal in birds and mammals show that increasing temporal variability in disturbance dynamics will favour dispersal rate. This supports the view that species associated with early successional stages may be good colonizers (Johnson & Gaines, 1990; McPeck & Holt, 1992). However, these models also show that increasing spatial variability in disturbance dynamics will select for lower dispersal rates. This is so because under this condition, new patches of suitable habitats are likely to appear nearby already

2 available habitats thus limiting the need to rely on long-distance colonization. As disturbance regime is often one of the main factors affecting changes in habitat availability at a landscape scale, the link between colonization processes and disturbance dynamics is likely to be of major importance (Johst *et al.*, 2002).

Fire is a major agent of disturbance in many systems. Due to hot and dry summers, fire has been closely linked to Mediterranean ecosystems and periodically affects extensive areas. Some Mediterranean-type shrublands are even thought to be maintained via recurrent wildfires (Moreno & Oechel, 1994). Wildfires affect habitats with different vegetation covers and structure making them converge towards structurally simpler and similar open vegetation that will progressively tend to resume its former structure (Pons & Prodon, 1996; Herrando *et al.*, 2002). Studies on bird communities have shown that new open areas are pioneered by bird species preferring open and low-vegetation habitat coexisting with species with strong site fidelity that were present before the fire (Lawrence, 1966; Izhaki & Adar, 1997; Imbeau *et al.*, 1999; Moreira *et al.*, 2001a; Barlow *et al.*, 2002). However, relatively little research has been focused on the spatial analysis of fire effects, such as the effect of disturbance extent on post-fire bird community composition or the mechanisms that determine colonization patterns of the new open habitats by pioneer species (Pons, 2002; Stuart-Smith *et al.*, 2002).

The objective of the present study was to assess to which degree the composition of post-fire bird colonizers was similar in several locations and constraint by dispersal. We use two main hypotheses. (A) Local dispersal to burned areas is a key factor behind bird colonization of areas affected by wildfires. In this case, we expect to find differences in the colonizer pool between locations, with such differences being mostly associated with pre-disturbance local abundance and landscape context. We also expect to find a lower occurrence of pioneer species in areas where potential local colonization sources are distant from disturbed sites. (B) Long-distance dispersal plays a major role on the colonization of post-fire habitats. Here, we predict post-fire species pools to be unrelated to pre-fire species abundance and landscape context. These hypotheses have strong implications in the spatial ecology of bird

communities of open areas because if hypothesis (A) holds true, species will be more likely to show metapopulation dynamics and be more sensitive to changes in the relative availability and isolation of suitable habitat patches in the landscape (Hanski, 1999).

To test these hypotheses, we used an innovative multi-scale approach which combines regional data derived from atlas work with local scale studies to analyse the factors that influence post-fire colonization of birds in Mediterranean landscapes affected by wildfires. We studied the post-fire colonization patterns of nine open-habitat species in eight recently burnt areas within the same biogeographical region. We then measured pre-disturbance potential colonization sources for each of the species to test to which degree these sources are associated with spatial differences in post-fire species occurrence and assess the spatial scale over which colonization patterns take place.

## METHODS

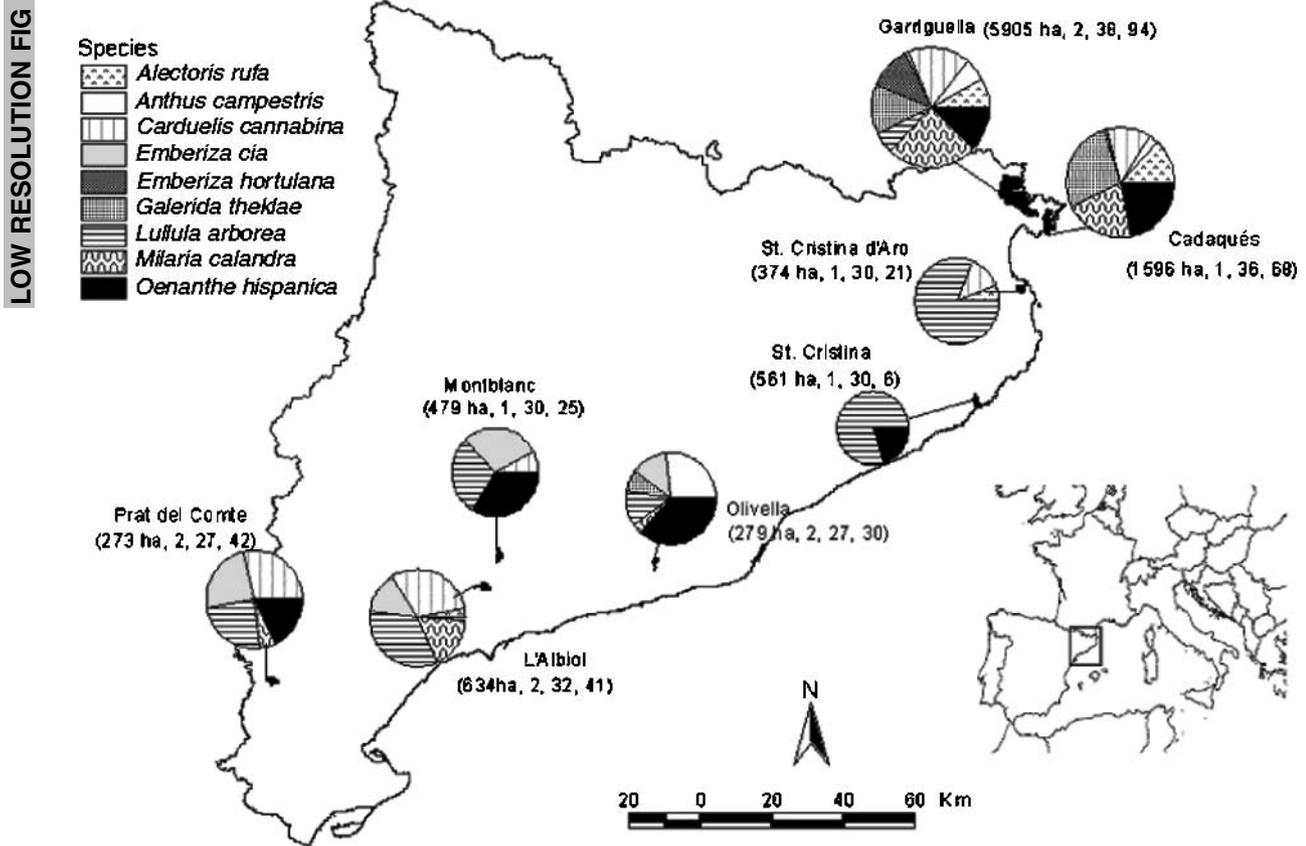
### Study area and site selection

The study was conducted in Catalonia, a region dominated by Mediterranean climate and located in the north-eastern corner of the Iberian Peninsula (Fig. 1). Our first aim was at identifying large wildfires that had affected an area of more than 250 ha within the 2 years prior to bird censuses. We selected large fires in order to minimize possible area effects influencing colonization of birds (Hanski, 1999). Secondly, large burnt areas maximize the probability of finding suitable habitats for most colonizer species.

Selected wildfires measured from 273 to 5905 ha, were at least 10 km from one another (Fig. 1) and were all located in mountain massifs with similar Mediterranean climatic conditions at low altitudes (100–500 m). All the burnt areas were formerly dominated by forest (mainly pine, cork–oak or holm–oak forests) and shrubland (calcareous garrigue or siliceous maquis) mosaics containing open habitats (clearings, old fields and dry grasslands) and rocky outcrops to variable extent. Fires took place in late winter (late January–early March) or in summer (June–August).

### Bird species

We selected nine species, typical of open habitats, that were especially abundant in previous studies on early post-fire avian communities in Catalonia (Pons & Prodon, 1996; Herrando *et al.*, 2002): *Alectoris rufa*, *Anthus campestris*, *Carduelis cannabina*, *Emberiza cia*, *Emberiza hortulana*, *Galerida theklae*, *Lullula arborea*, *Miliaria calandra* and *Oenanthe hispanica*. Once site-tenacious forest species are excluded, these nine species represent the bulk of the bird community occupying new habitats created by fire (Pons & Prodon, 1996; Herrando *et al.*, 2002). Therefore, all can potentially occur during the first years after fire in burned shrubland, in burned forest or in both. In contrast, the nine



**Figure 1** Geographical location of the eight wildfires studied. Pie charts show the relative contribution of each of the selected colonizer focal species to the total of presences detected in each fire. For each fire, we show in brackets: total area in hectares, number of years after fire prior to post-disturbance censuses, total number of censused periods and total number of individuals of the nine analysed species recorded during independent periods. The map on the lower right corner shows the location of the study region, Catalonia, in the north-east corner of the Iberian Peninsula.

species are very scarce or completely absent from habitats with developed vegetation cover and therefore absent from most of the habitats present in a given area before being affected by a forest fire.

### Field methods

For each fire, we conducted bird censuses during the first or second breeding season (May–June, 2002 or 2003) after the fire. Within each fire perimeter, we established a series of line transects (2–5) without limited census belts but restricted to birds positively occurring in burnt habitats. Transects were walked once during the morning by a single observer (mostly P.P.) at a speed of about  $2 \text{ km h}^{-1}$  (Bibby *et al.*, 1992). They were located with the aim of recording all the focal species under study on the premise that they had to traverse burnt habitats. Usually this was not difficult because, due to the reduced cover, the observer was not restricted to pathways existing before the fire. Unburnt areas, agricultural habitats and fire edges when possible, were not censused. For six fires up to 700 ha, the area surveyed by our transects

covered almost completely the burned area. For the two largest fires (> 1500 ha) it was impossible to do this without a disproportionate sampling effort and therefore, transects were walked in a number of representative locations covering different areas. We divided each transect into 15-min periods, rather than fixing a constant length for each sampling unit. This allowed us an easier standardization of sampling periods in the field. In order to keep the number of periods between fires comparable, the minimum number of periods was fixed to 25 and increased progressively to cover the needs of spatial representation in bigger fires. This made a total of 27–39 periods per burnt area (see Fig. 1 for details on sampling effort). Within each of these periods, we did not count birds but just noted the occurrence (presence or absence) of any of the focal species either seen or heard. Thus, the raw data obtained per fire and species was frequency of occurrence (e.g. total number of occurrences given a number of periods). In order to avoid serial dependence in species occurrence between adjacent 15-min periods, we divided each transect into two sets of consecutive periods and selected the set with the higher number of

occurrences per species. The final sampling unit obtained per fire and species was the total number of occurrences given a number of periods. With this method, we made sure that no focal species were missed during the process of data handling while minimizing the risk of double recording the same individual in adjacent periods.

### Estimation of habitat suitability prior to fires

Detailed, quantitative estimation of potential population sources at regional scales are often unavailable. It is only recently that such faunal information has become available through atlas works conducted at regional and national scales. Here, we used species habitat suitability maps (HSM) generated by the new Catalan Breeding Bird Atlas (Estrada *et al.* unpublished data) to estimate potential population source areas for the focal species within and around the areas affected by the studied fires. HSM were generated from autologistic models predicting species presence in  $1 \times 1$  km squares. These models linked the occurrence of species in 3140  $1 \times 1$  km squares, evenly distributed throughout Catalonia and that covered *c.* 9% of the country area (*c.* 32,000 km<sup>2</sup>), to information about land use and climate that was contained in 42 generated environmental variables and three autologistic terms (accounting for spatial autocorrelation in species distribution). With this approach we generated probability surfaces that can be extrapolated to the whole extent of the region from which such environmental data are also available (Augustin *et al.*, 1996; Guisan & Zimmermann, 2000; Brotons *et al.*, 2004). HSM models were calibrated on 70% of the data available (3140 sampling squares) and evaluated on the remaining 30%. The evaluation of the models by means of ROC curve (Fielding & Bell, 1997) for the nine species included in the analysis showed the models had high predictive accuracy (0.79–0.93). Final grid projections of habitat models were smoothed to a resolution of 500 m and represented probability of species occurrence within each square.

Although the probability of successful colonization of new habitat patches depends on many factors specific to particular species and environments, propagule size or the number of potential migrants arriving at an empty patch is likely to be a key factor (Hanski, 1999). We used species HSM to estimate potential colonizer sources for each fire. We first generated three buffer zones at 5, 10 and 20 km distance from each fire perimeter. We calculated a series of variables for the area between fire perimeter and each of the buffered distances (referred to by using the number describing buffer distance). The same variables were also calculated for the area within the fire perimeter itself (referred to as zero distance). Based on preliminary analyses of their potential as estimators of colonizer sources, we assessed the following variables for each species in each of the four buffered areas: maximum value of habitat suitability (MaxHS), mean value of habitat suitability (MeanHS) and total sum of habitat suitability values (SumHS). Sea was considered to have zero

probability of occurrence for all the species considered, whereas emerged lands areas outside the political boundaries of Catalonia were considered as 'no data' in the buffer estimations. Unfortunately, at the moment there is no data on quantitative species distribution from areas adjacent to Catalonia. However, there are no remarkable discontinuities in relief or land use changes along the border with adjacent territories to the north and west that could bias estimation of colonizer sources around fires. The use of these variables was justified as they can be considered as estimators of the presence of high quality areas (i.e. maximum values of habitat suitability) or the mean overall suitability of the area under examination (i.e. mean and sum of values of habitat suitability) for a given species. Finally, atlas data for one of the fires used in our study (Garriguella) were collected mainly after the fire event, which prevented its use in analyses linking local colonizer occurrence and regional potential colonizer sources.

### Statistical analysis

We used the Renkonen percentage similarity index (Legendre & Legendre, 1998) to quantify post-fire patterns of species occurrence in the different fire locations and Mantel tests (Legendre & Legendre, 1998) to determine whether similarity in species occurrence was associated with the distance between fire locations. Overall differences in the frequency of occurrence of species in different fires were tested by means of log-linear models. In particular, we tested whether the interaction between species and fire location helped explain species distribution by fitting all two-way interactions to the data (Legendre & Legendre, 1998).

We used generalized linear modelling (GLM) on post-fire species occurrence to test for the effects of potential sources of colonization within and around each fire. Instead of using the frequency of occurrence per species, which loses information on sample size from which the proportion is estimated, we used the number of occurrences per species and fire as the response variables and the number of independent periods censused per fire as the binomial denominator in a model with binomial error and a logit link function (McCullagh & Nelder, 1989). For each GLM model fitted, we estimated the adjusted generalized coefficient of determination ( $\tilde{R}^2$ ). This coefficient ranges between 0 and 1 and is a generalization of the coefficient of determination for linear regression (Nagelkerke, 1991). When GLM models were affected by overdispersion we applied Williams procedure (McCullagh & Nelder, 1989).

We first used a univariate approach to determine the strength of the association between occurrences of post-fire colonizer and variables of potential sources of colonization at different spatial scales. Using the most significant variables at a given radius, we tested for interaction effects between species and fire location. Finally, we ran univariate tests for each species to determine the appropriate scale of possible effects of colonization sources on species occurrence.

## RESULTS

### Post-fire colonizer similarity across fires

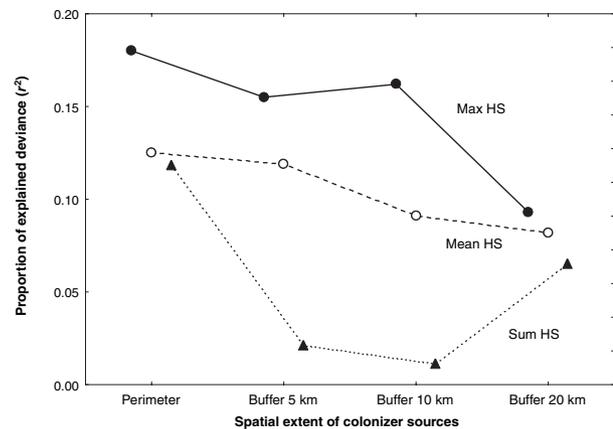
We analysed eight fires of adequate size which contained a minimum of two and a maximum of nine colonizer species (Fig. 1). Post-disturbance similarity in patterns of species occurrence between fires was rather low [Renkonen percentage similarity index of  $0.42 \pm 0.17$  on average; minimum = 0.19 (Montgrí-Cadaqués fires); maximum = 0.80 (Montgrí-St Cristina fires; Fig. 1)]. Similarity of species occurrence patterns did not decrease with increasing geographical distance (Mantel test,  $r = 0.26$ ,  $P = 0.10$ ). The lack of significant species spatial autocorrelation was mainly due to low similarity between the species-rich northern burned areas (highest number of species of all fires; eight and nine species) and the nearby species-poor burned areas of St Cristina and Montgrí (two and three species). When excluding the two northern fires (Cadaqués and Garriguella) from the analysis, the similarity of species occurrence patterns significantly decrease with increasing geographic distance (Mantel test,  $r = 0.66$ ,  $P = 0.001$ ).

The lack-of-fit of the log-linear model, including all two-way interactions between species occurrence and fire location ( $\chi^2 = 325.20$ , d.f. = 56,  $P < 0.0001$ ), indicates that post-fire differences in colonizer composition between burned areas were significant. It follows that dependence between fire and species was necessary to explain occurrence patterns within our data set. The differences between fires were maintained even when the analysis was repeated without the two northern fires ( $\chi^2 = 114.30$ , d.f. = 40,  $P < 0.001$ ).

### Colonizer occurrence and potential source areas

Univariate tests on the hypothetical association between patterns of post-fire species occurrence and potential source areas as estimated by habitat suitability models showed that MaxHS within fire perimeter was the best single significant predictor of the probability of species occurrence after fire (Fig. 2). There was a general pattern for MaxHS, MeanHS and partially for SumHS to decrease the strength of the association with post-fire colonization patterns in progressively larger buffer areas around the fire perimeter (Fig. 2). The same pattern was evident even when the Cadaqués fire, was omitted from the analyses (MaxHS within the fire perimeter,  $\bar{R}^2 = 0.15$ ,  $\chi^2 = 17.73$ , d.f. = 1,  $P < 0.00001$ , other buffer distances not shown).

Using the preliminary univariate analysis as a guide, we analysed interactions between MaxHS and patterns of species colonization. The association of MaxHS with patterns of species colonization was consistent across species (Interaction, Species \* MaxHS,  $\chi^2 = 10.58$ , d.f. = 8,  $P = 0.23$ , Fig. 3) and fire location (Interaction, Fire \* MaxHS,  $\chi^2 = 7.034$ , d.f. = 6,  $P = 0.32$ , Fig. 4). Furthermore, whether the post-fire census of a bird community had been conducted 1 or 2 years after a fire did not have a noticeable effect on the overall post-fire



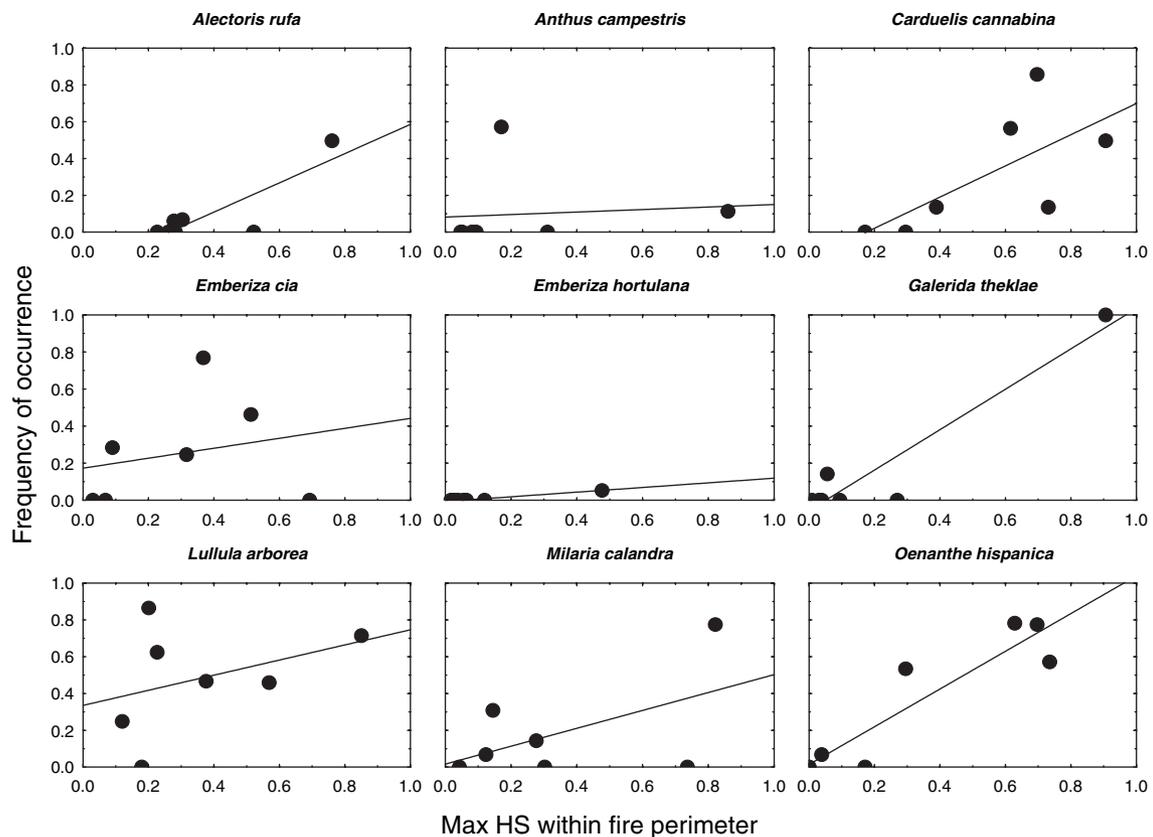
**Figure 2** Strength of the association between species frequency of occurrence and estimated potential colonization sources prior to the fire as derived from atlas data (MaxHS, maximum, MeanHS, mean value and SumHS, overall sum of probability of species presence within each buffered distance) for all nine focal species combined.

colonizer occurrence (Effect Year,  $\chi^2 = 1.15$ , d.f. = 1,  $P = 0.28$ ) nor on the overall impact of MaxHS on such variable (Interaction, Year \* MaxHS,  $\chi^2 = 0.20$ , d.f. = 1,  $P = 0.65$ ).

A more detailed analysis per species indicated that the relationship between the occurrence of colonizers and potential source areas (MaxHS) was stronger when the later was estimated within the fire perimeter (*A. rufa*, *G. theklae*, *M. calandra* and *O. hispanica*; Fig. 5), except for two species *C. cannabina* and *E. cia* which showed stronger relationships when 5 or 10 km buffers were respectively used (Fig. 6). For three of the species *A. campestris*, *L. arborea* and *E. hortulana*, the positive relationship between post-fire occurrence and potential colonizer sources was never significant (Fig. 5).

## DISCUSSION

Our results showed strong significant differences in the post-fire occurrence of colonizer species between geographically distinct sites in Catalonia. Burned areas within perimeters that had a low proportion of habitat suitable for the species of interest before the fire had less species and lower species occurrence in the habitat patches created by fire. The occurrence of colonizers in burned areas was associated with the sources of colonizers near the burned areas, suggesting that the species studied mainly rely on short distance dispersal to colonize recently burned areas. These results do not support the hypothesis that early successional stages and open habitats should have homogeneous community structure at a regional scale because of the strong ability of their species to colonize (colonizer syndrome). Our results support the hypothesis that local scale rather than regional scale ecological processes determine bird colonization of post-fire habitats in Mediterranean landscapes.



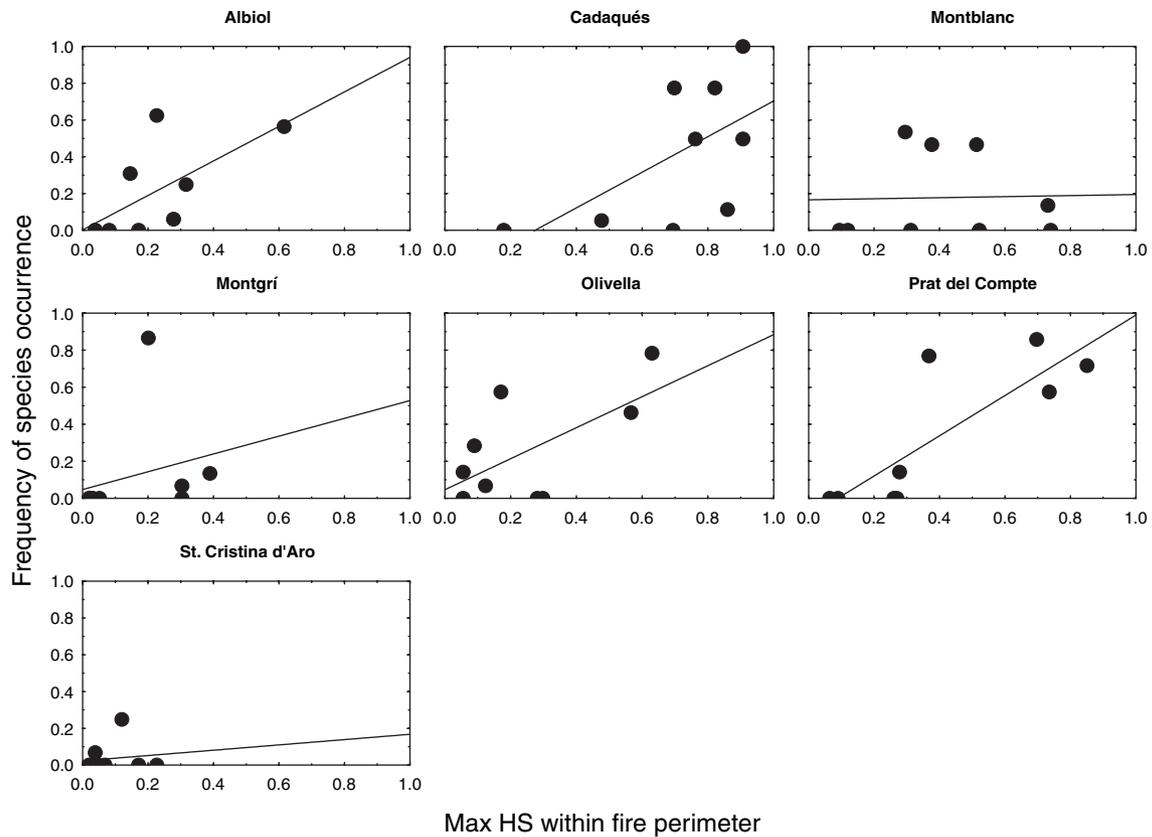
**Figure 3** Relationship between post-fire species frequency of occurrence and estimated potential colonization sources prior to the fire as derived from atlas data (MaxHS, maximum probability of species presence within fire perimeter) for each of the nine focal species included in the study.

### Local vs. regional colonization processes

Unless disturbances periodically created suitable habitat, species which live in ephemeral habitats (such as those commonly found in early stages of succession) have necessarily ephemeral local populations (Jenkins & Buikema, 1998). Such species can only survive at the metapopulation level by having a migration rate sufficiently high to enable the continuous establishment of new populations (Johnson, 1969). At a regional scale, birds of open habitats may function as a metapopulation driven by the interplay of succession and disturbance. Wildfires generate the habitats needed by pioneer species but the colonization of such appearing patches is strongly constrained by dispersal. Although our results supported the hypothesis of local factors as main drivers of colonization processes in birds in post-fire open habitats, we envisage colonization as a multiscale process in which processes acting at larger scales certainly play a significant role. We showed that high densities of post-fire colonizers are associated with pre-fire high habitat suitability in the area. This might suggest that above a certain local abundance threshold, post-disturbance colonization is mostly a local process possibly including some degree of site tenacity as shown for shrubland and forest birds after fire (Petersen & Best, 1987; Wooller & Calver, 1988; Pons, 1998). As species local abundance becomes

smaller, the probability of post-disturbance local colonization and persistence also decrease while the influence of stochastic processes acting at larger spatial scales such as long-distance colonization of new patches increases. These population mechanisms would eventually lead to spatial stability in highly suitable areas, whereas in areas with low availability of potential colonization sources, the population dynamics at new available habitats will be probably governed by metapopulation processes (Real, 2000; Lens *et al.*, 2002). Here isolation would pose difficulties to colonization but does not prevent it. This is illustrated by anecdotal long-distance colonization events in our data set (e.g. *O. hispanica* in St Cristina fire for which the closest population was more than 50 km away). From our present data such events seem of secondary importance in determining general colonization patterns.

Our results on the factors behind post-fire bird colonization suggest that landscape context is likely to play a major role in controlling species-colonizing processes on new open areas. Particularly, fires affecting previous heavily forested areas unsuitable for birds of open habitats would have more difficulties to be colonized than those areas already providing nearby suitable habitats for those species. Limitations posed to individual movement by landscape configuration is relatively well known in forest passerines (Desrochers & Hannon, 1997),



**Figure 4** Relationship between post-fire species frequency of occurrence and estimated potential colonization sources prior to the fire as derived from atlas data (MaxHS, maximum probability of species presence within fire perimeter) for each of the seven fires for which this relationship could be measured.

but it has been often neglected in species of open habitats associated with disturbance due to the assumption that this species rely on dispersal to colonize appearing habitats. In this context, habitat heterogeneity at a local scale appears as a major factor (Dunning *et al.*, 1992), as the maintenance of suitable open habitats within a matrix of shrubby and forest habitats may greatly enhance colonization capabilities of species after forest fires (Frouz & Kindlmann, 2001; Murphy, 2001).

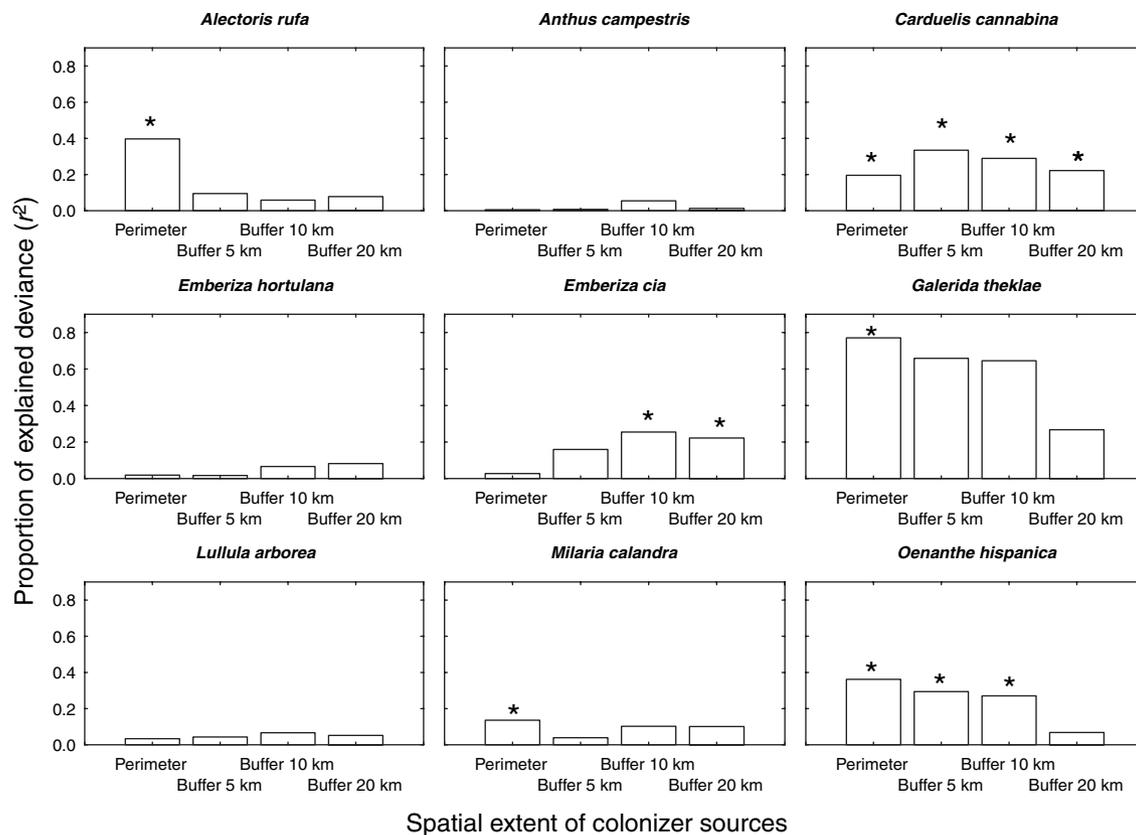
### Disturbance and biogeography

Mediterranean landscapes are highly dynamic and disturbances such as wildfires are likely to be part of the evolutionary constraints of life-history traits of most Mediterranean species (Blondel & Aronson, 1999). If these were to be true, we would expect Mediterranean species to respond to such high disturbance rate of the system with an adaptation to short-distance dispersal maximizing colonization perspectives with minimal costs. This hypothesis is supported by theoretical models that show how increasing spatial variability in habitat dynamics may lead to selection for a reduction in the rate of dispersal (Travis & Dytham, 1999). Although more detailed analysis on this issue would be necessary, our data seem to

support this view as species of primarily Mediterranean distribution such as *G. theklae*, *O. hispanica* or *A. rufa* (Prodon, 1993) showed the strongest influence of local scale processes on colonization patterns. Differences in habitat and landscape responses linked to species biogeographical origin have been previously described in Mediterranean bird communities, (Shochat *et al.*, 2001; Suarez-Seoane *et al.*, 2002) and suggest this factor as an important issue for future investigation if we aim at predicting species-specific ecological changes in the context of anthropogenic global change.

### Forest fires and landscape change trends in the Mediterranean

Human influence is likely to be a capital factor indirectly affecting the processes guiding post-fire colonization of Mediterranean open habitats. First, around the Mediterranean basin, succession and disturbance agents (mainly fire, farming and grazing) are heavily linked to human activities. Secondly, through a semi-permanent disturbance regime in grazing agricultural areas and provided they are a low-intensity use (Donald *et al.*, 2001), human activities may create habitat patches for open-habitat species assuring a permanent availability of suitable habitat at a landscape scale. However, in



**Figure 5** Strength of the association between species frequency of occurrence and estimated potential colonization sources prior to the fire as derived from atlas data (MaxHS, maximum probability of species presence) at different spatial scales ranging from the area within each fire perimeter to the buffer of 20 km around each fire (see Fig. 2). Stars represent significance at  $P < 0.05$ .

areas in which traditional agricultural activity is progressively being abandoned, fire is becoming the most important factor maintaining availability of open habitats (Moreira *et al.*, 2001b).

Fire recurrence may play an important role here by increasing the probability that suitable areas remain for open-habitat birds. At present, forest fires also play a major role in introducing heterogeneity at a landscape scale in Mediterranean landscapes (Lloret *et al.*, 2002). However, this process is not isolated in influencing landscape pattern and agriculture, and extensive livestock abandonment also leads to vegetation recovery and landscape homogenization and seems to counterbalance the effect of fires in these landscapes (Preiss *et al.*, 1997; Moreira *et al.*, 2001a). Habitat heterogeneity may become crucial for maintenance of species of open habitats associated with perturbation dynamics creating such habitats. Current trends in landscape change in the north-western Mediterranean towards a progressive homogenization and afforestation of landscapes point towards a lower overall suitability of areas for open-habitat birds which will experience a progressive isolation of their habitats posing difficulties for colonization of new appearing, post-disturbance open habitats.

A progressive increase in the total number of wildfires has been recorded in Catalonia due to an accumulation of plant

matter after rural abandonment, increased use of forest for recreational uses and increasing temperature resulting in a higher number of days of wildfire risk (Piñol *et al.*, 1998). In recent years, active fire-control policies have been largely implemented leading to a higher effectiveness in fire detection and suppression at early stages. However, at present, a very small proportion of forest fires that cannot be controlled at such early stages (<8%) are responsible for *c.* 80–90% of the burnt surface. This is inducing the homogenization of the large tracts of the territory to a single land use (Lloret *et al.*, 2002). If the hypothesis of local population dynamics controlling colonization processes in Mediterranean areas holds true, the effects of wildfires on such species will depend on the frequency and extent of affected areas. If small and medium-sized forest fires prevail at long term, local scale heterogeneity introduced in the landscape may favour metapopulation dynamics for most of this species by maintaining a dynamic pool of suitable habitat patches that are colonized after perturbation by nearby suitable habitats. On the contrary, a spread of extensive wildfires will initially favour open-habitat birds, but the habitat may soon turn unsuitable until new perturbations generate open habitats again. In the light of our results, the population benefits derived from colonization of recently burnt areas by threatened open-habitat birds seem

lower than previously thought (Prodon, 1987) if such new areas are relatively distant from potential colonizer sources. A progressive increase in source population isolation may be originated if large forest fires affect the same area repeatedly at sufficient time intervals of 20 years or more (Herrando *et al.*, 2002). At present very few data are available on the effects of forest fire regime on population dynamics of open-habitat birds at regional and landscape scales and further examination including a modelling approach is warranted.

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## REFERENCES

- Augustin, N.H., Muggleston, M.A. & Buckland, S.T. (1996) An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology*, **33**, 339–347.
- Baker, H.G. & Stebbins, G.L. (1977) *The genetics of colonizing species*. Academic Press, New York.
- Barlow, J., Haugeaasen, T. & Peres, C.A. (2002) Effects of ground fires on understorey bird assemblages in Amazonian forests. *Biological Conservation*, **105**, 157–169.
- Bibby, C., Burguess, N.D. & Hill, D.A. (1992) *Bird census techniques*. Cambridge University Press, Cambridge.
- Blondel, J. & Aronson, J. (1999) *Biology and wildlife of the Mediterranean region*. Oxford University Press, Oxford.
- Brawn, J.D., Robinson, S.K. & Thompson, F.R. (2001) The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics*, **32**, 251–276.
- Brotons, L., Thuiller, W., Araújo, M.B. & Hirzel, A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, **27**, 437–448.
- Buddle, C.M., Spence, J.R. & Langor, D.W. (2000) Succession of boreal forest spider assemblages following wildfire and harvesting. *Ecography*, **23**, 424–436.
- Desrochers, A. & Hannon, S.J. (1997) Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology*, **11**, 1204–1210.
- Donald, P.F., Green, R.E. & Heath, M.F. (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268**, 25–29.
- Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65**, 169–175.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Frouz, J. & Kindlmann, P. (2001) The role of sink to source re-colonisation in the population dynamics of insects living in unstable habitats: an example of terrestrial chironomids. *Oikos*, **93**, 50–58.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hanski, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford.
- Herrando, S., Brotons, L., Del Amo, R. & Llacuna, S. (2002) Bird community succession after fire in a dry Mediterranean shrubland. *Ardea*, **90**, 303–310.
- Hutchinson, G.E. (1951) Copepodology for the ornithologist. *Ecology*, **32**, 571–581.
- Imbeau, L., Savard, J.P.L. & Gagnon, R. (1999) Comparing bird assemblages in successional black spruce stands originating from fire and logging. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **77**, 1850–1860.
- Izhaki, I. & Adar, M. (1997) The effects of post-fire management on bird community succession. *International Journal of Wildland Fire*, **7**, 335–342.
- Jenkins, D.G. & Buikema, A.L. (1998) Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs*, **68**, 421–443.
- Johnson, C.G. (1969) *Insect migration and dispersal by flight*. Methuen, London.
- Johnson, M.L. & Gaines, M.S. (1990) Evolution of dispersal – theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics*, **21**, 449–480.
- Johst, K., Brandl, R. & Eber, S. (2002) Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos*, **98**, 263–270.
- Lavelle, S., Rochette, C. & Lebreton, J. D. (1999) Functional groups for response to disturbance in Mediterranean old fields. *Oikos*, **84**, 480–498.
- Lawrence, G.B. (1966) Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. *Ecology*, **47**, 278–291.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier, Amsterdam.
- Lens, L., Van Dongen, S., Norris, K., Githiru, M. & Matthysen, E. (2002) Avian persistence in fragmented rainforest. *Science*, **298**, 1236–1238.
- Lloret, F., Calvo, E., Pons, X. & Diaz-Delgado, R. (2002) Wildfires and landscape patterns in the Eastern Iberian peninsula. *Landscape Ecology*, **17**, 745–759.

- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*. Chapman & Hall, London.
- McPeck, M.A. & Holt, R.D. (1992) The evolution of dispersal in spatially and temporally varying environments. *American Naturalist*, **140**, 1010–1027.
- Moreira, F., Ferreira, P.G., Rego, F.C. & Bunting, S. (2001a) Landscape changes and breeding bird assemblages in northwestern Portugal: the role of fire. *Landscape Ecology*, **16**, 175–187.
- Moreira, F., Rego, F.C. & Ferreira, P.G. (2001b) Temporal (1958–1995) pattern of change in a cultural landscape of northwestern Portugal: implications for fire occurrence. *Landscape Ecology*, **16**, 557–567.
- Moreno, J.M. & Oechel, W.C. (1994) *The role of fire in Mediterranean-type ecosystems*. Springer-Verlag, New York, p. 201.
- Murphy, M.T. (2001) Source–sink dynamics of a declining Eastern Kingbird population and the value of sink habitats. *Conservation Biology*, **15**, 737–748.
- Nagelkerke, N.J.D. (1991) A note on a general definition of the coefficient of determination. *Biometrika*, **78**, 691–692.
- Petersen, K.L. & Best, L.B. (1987) Effects of prescribed burning on nongame birds in a Sagebrush community. *Wildlife Society Bulletin*, **15**, 317–329.
- Pickett, S.T.A., Kolasa, J., Armesto, J.J. & Collins, S.L. (1989) The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos*, **54**, 129–136.
- Piñol, J., Terradas, J. & Lloret, F. (1998) Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change*, **38**, 345–357.
- Pons, P. (1998) Bird site tenacity after prescribed burning in a Mediterranean shrubland. *Fire management and landscape ecology* (ed. by L. Traubad), Fairfield, Washington.
- 4 Pons, P. (2002) The population responses of birds to fire in Mediterranean ecosystems. *Fire, landscape and biodiversity: an appraisal of the effects and effectiveness* (ed. by G. Pardini and J. Pintó), pp. 57–68. Servei de Publicacions de la Universitat de Girona, Girona.
- Pons, P. & Prodon, R. (1996) Short term temporal patterns in a Mediterranean shrubland bird community after wildfire. *Acta Oecologica*, **17**, 29–41.
- Preiss, E., Martin, J.L. & Debussche, M. (1997) Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. *Landscape Ecology*, **12**, 51–61.
- Prodon, R. (1987) Incendies et protection des oiseaux en France méditerranéenne. *L'Oiseau et la Revue Française d'Ornithologie*, **57**, 1–12.
- Prodon, R. (1993) Une alternative aux 'types biogéographiques' de Voous: la mesure des distributions latitudinales. *Alauda*, **62**, 83–90.
- Real, J. (2000) Wildfires could favour Black Wheather *Oenanthe leucura* recolonisation. *Ardeola*, **47**, 93–96.
- Shochat, E., Abramsky, Z. & Pinshow, B. (2001) Breeding bird species diversity in the Negev: effects of scrub fragmentation by planted forests. *Journal of Applied Ecology*, **38**, 1135–1147.
- Stuart-Smith, K., Adams, I.T. & Larsen, K.W. (2002) Songbird communities in a pyrogenic habitat mosaic. *International Journal of Wildland Fire*, **11**, 75–84.
- Suarez-Seoane, S., Osborne, P.E. & Baudry, J. (2002) Responses of birds of different biogeographic origins and habitat requirements to agricultural land abandonment in northern Spain. *Biological Conservation*, **105**, 333–344.
- Travis, J.M.J. & Dytham, C. (1999) Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 723–728.
- Wooler, R.D. & Calver, M.C. (1988) Changes in an assemblage of small birds in the understorey of dry sclerophyll forest in southwestern Australia after fire. *Australian Wildlife Research*, **15**, 331–338.

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