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Aridity, fire severity and proximity of populations affect the temporal responses of open-habitat birds to wildfires

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ABSTRACT

The loss of open habitats in Europe has led to severe declines in birds associated with these habitats. However, certain ecological disturbances reverse the trend towards afforestation and create appropriate conditions for open-habitat species. Yet, open-habitat bird occupancy dynamics after disturbance depend on a complex combination of as-yet poorly studied factors. We analysed the colonization patterns and post-fire time-window of occurrence of open-habitat species along 687 transects in 68 burnt areas over a period of 11 years. During the study, 8345 individuals belonging to 22 open-habitat birds were detected. Species richness was related to an increased time elapsed since the fire, fire severity and proximity of potential population sources. Many species changed across the 11 years post-fire. Some species like the tawny pipit and the ortolan bunting, showed time lags affecting the timing of local extinction. Water deficit played a significant role in bird occurrence and six species benefited from drier conditions. Open-habitat species were more frequently detected in burnt areas near previously occupied areas and in severely burnt areas. Our results support the hypothesis that fire plays a critical role in the distribution dynamics of open-habitat species. Peak number of species was reached rapidly, between two and 6 years after fire, although a few species showed their peak abundance later on. An appropriate strategy for favouring open-habitat specialists in these landscapes, while reducing the risk of large wildfires, should prioritize integrated fire management to generate patches of different fire ages.

1. Introduction

Open habitats declined in Europe in the mid-twentieth century (Stoate et al., 2009). Declines were mainly due to two contrasting trends, namely, agricultural intensification in lowlands and land abandonment in upland areas (Donald et al., 2001; Reif and Hanzelka, 2020). The loss of these open habitats has led to a widespread decline in open-habitat bird species (Benton et al., 2003; Donald et al., 2001), defined as a set of species that are restricted or prefer grasslands, agricultural lands (farmlands) and other habitats with sparse or low vegetation cover. Consequently, open-habitat species are overrepresented on threatened bird lists in Europe (BirdLife International, 2004). However, this pattern is not restricted to birds since butterfly, reptile and mammal populations in open-habitats exhibit similar trends (Delibes-Mateos et al., 2009; Herrando et al., 2016; Moreira and Russo, 2007; Warren et al., 2021). Today, most semi-natural open habitats are present only as fragments within a matrix of forest and/or intensive farming, which can severely affects the dispersal ability of organisms, and condemn populations to increasing isolation and, eventually, local extinction (Haddad et al., 2015; Tilman et al., 1994). Semi-natural habitats (shrubland or woodlands) are relatively permanent habitats, and are considered the key source of biodiversity in agricultural landscapes (Billeter et al., 2008) by providing over-wintering sites, food resources, refuges, and source populations for re-colonization of disturbed habitats (Raderschall et al., 2021). Yet, natural disturbances (e.g. wildfires, floods, storms and snow avalanches), forest exploitation or prescribed burning may in fact promote the occurrence of open-habitat birds within this vegetation matrix (Ram et al., 2020; Thorn et al., 2016; Żmihorski et al., 2016).

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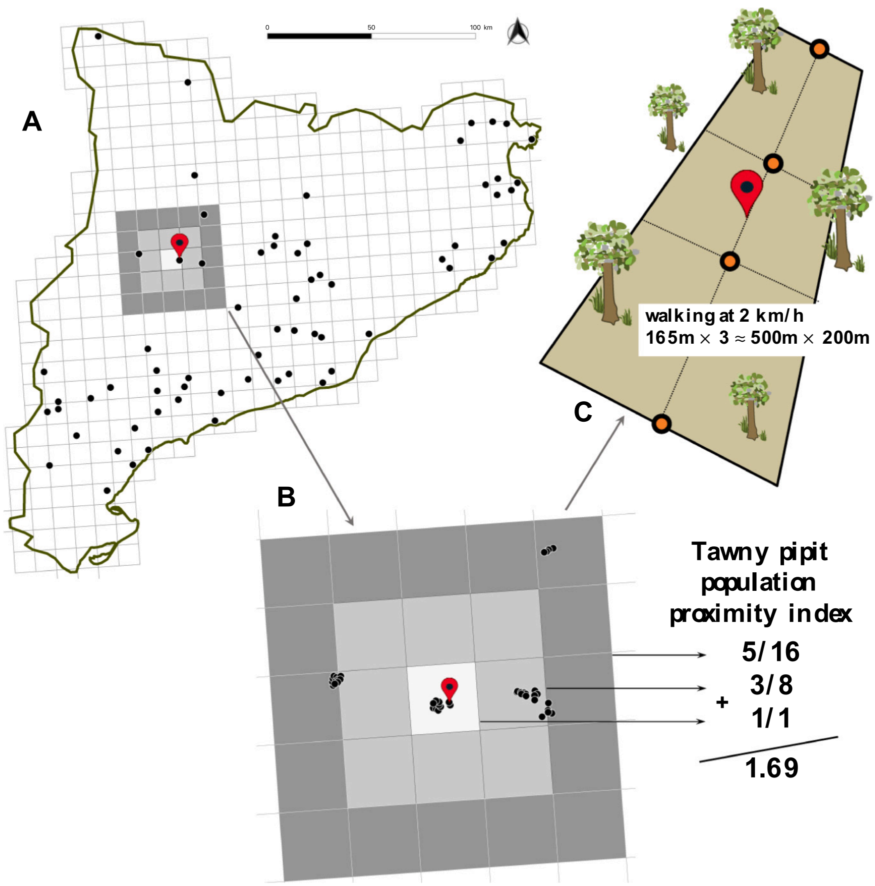

Fig. 1. Site location and sampling design scheme. Location and distribution of (A) the 68 (black points) burnt areas in Catalonia. (B) Example of calculation of the Tawny pipit population proximity index, showing black dots for transect locations (found in four burnt areas in this example) and the three buffers of 10 × 10 km squares (grey gradient). Each buffer takes a maximum colonization value of 1, being 0 and 3 the minimum and maximum sum of the index. (C) Representation of a bird sampling transect, with three 165 m × 200 m bands and four points where the fire severity was visually assessed.

Table 1

Effect of the time since the fire and water deficit interaction on open-habitat bird community.

Summary the effects of the time since the fire and water deficit interaction models derived from generalized lineal mixed models (GLMM) analyses, of open-habitat species richness and 19 open-habitat species occurrences in 68 burnt areas distributed throughout Catalonia ranging in size from 51 to 6647 ha, affected by wildfires in 2000–2011.

Scientific name	Common name	Intercept	TSF	WD	TSF * WD
Open-habitat species richness		**0.3 ± 0.14***	**0.07 ± 0.01*****	0.0004 ± 0.0004	0.00006 ± 0.00005
Alectoris rufa	Red-legged partridge	**−2.89 ± 0.44*****	−0.02 ± 0.06	−0.0002 ± 0.002	0.0003 ± 0.0003
Anthus campestris	Tawny pipit	**−2.68 ± 0.49*****	**−0.17 ± 0.08***	−0.0009 ± 0.002	0.0004 ± 0.0003
Carduelis cannabina	Common linnet	**−2.67 ± 0.26*****	**0.19 ± 0.03*****	**0.003 ± 0.0009***	**−0.0002 ± 0.0001***
Coturnix coturnix	European quail	**−15.55 ± 2.98*****	**1.23 ± 0.3*****	**0.02 ± 0.008***	**−0.004 ± 0.001***
Emberiza calandra	Corn bunting	**−5.56 ± 0.*****	**0.66 ± 0.08*****	0.005 ± 0.003	**−0.001 ± 0.0003*****
Emberiza cia	Rock bunting	**−1.67 ± 0.58****	−0.08 ± 0.08	**−0.008 ± 0.002*****	0.0005 ± 0.0003
Emberiza hortulana	Ortolan bunting	**−8.18 ± 1.64*****	0.14 ± 0.1	**−0.01 ± 0.005****	0.0003 ± 0.0006
Falco tinnunculus	Common kestrel	**−4.99 ± 0.61*****	0.17 ± 0.09	**0.004 ± 0.002***	−0.0005 ± 0.0004
Galerida cristata	Crested lark	**−10.33 ± 2.42*****	0.18 ± 0.12	**0.01 ± 0.007***	−0.00006 ± 0.0005
Galerida theklae	Thekla's lark	**−6.5 ± 0.75*****	0.01 ± 0.07	**0.01 ± 0.002*****	0.0003 ± 0.0002
Lanius meridionalis	Iberian grey shrike	**−9.33 ± 0.002*****	0.11 ± 0.09	−0.003 ± 0.001	0.0005 ± 0.0004
Lanius senator	Woodchat shrike	**−2.56 ± 0.41*****	0.04 ± 0.05	0.001 ± 0.002	−0.0002 ± 0.0002
Lullula arborea	Woodlark	**−0.99 ± 0.42***	−0.03 ± 0.05	−0.00001 ± 0.001	0.00006 ± 0.0002
Oenanthe hispanica	Western black-eared wheatear	**−4.78 ± 0.58**	−0.03 ± 0.07	**0.01 ± 0.002*****	0.0003 ± 0.0003
Oenanthe leucura	Black wheatear	**−8.91 ± 1.85*****	0.02 ± 0.28	0.009 ± 0.005	−0.0002 ± 0.0008
Petronia petronia	Rock sparrow	**−5.77 ± 0.84*****	**0.25 ± 0.11***	0.0005 ± 0.003	−0.0004 ± 0.0004
Phoenicurus ochruros	Black redstart	**−5.08 ± 1.6****	−0.39 ± 0.22	**−0.03 ± 0.006*****	**0.003 ± 0.001****
Saxicola torquata	European stonechat	**−1.46 ± 0.36*****	**0.16 ± 0.05****	**−0.006 ± 0.001*****	**0.0007 ± 0.0002****
Upupa epops	Eurasian hoopoe	**−4.52 ± 0.63**	0.03 ± 0.09	0.002 ± 0.002	0.0001 ± 0.0003

The table shows the model parameter coefficient, its standard error (±SE) and the associated *p*-values:

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

Disturbances can locally reverse afforestation processes by modifying or creating appropriate conditions for open-habitat species. The dynamics of open-habitat bird occupancy after disturbance will always depend on a combination of factors, most as yet poorly understood.

The colonization of a new appropriate site implies a sequence of dispersal, establishment and survival of individuals, as well as the

Table 2
Effect of environmental variables on open-habitat bird community.
Summary of final models derived from generalized additive mixed models (GAMM) analyses, of open-habitat species richness and 19 open-habitat species occurrences in 68 burnt areas distributed throughout Catalonia ranging in size from 51 to 6647 ha, affected by wildfires in 2000–2011. If the variable was included in the final model but was not-significant, only the coefficient sign (+ or –) is showed. Intercept is the value of oak pre-fire habitat when all the other covariates are = 0, while *p* value indicates whether it is significantly different from 0.

Scientific name	Common name	Intercept	Smoothed term for TSF (edf)	Water deficit	Pre-fire habitat		Fire severity	Fire size	Population proximity index	
					Pine	Shrubland			latitudinal	aridity
Open-habitat species richness		1.0 ± 0.39**	5.28**	(−)	(−)	(−)	0.06 ± 0.01***	(+)		−0.08 ± 0.02**
Alectoris rufa	Red-legged partridge	−6.86 ± 2.76*	2.57*	(−)	(−)	(+)	(−)	(+)	(+)	
Anthus campestris	Tawny pipit	−5.23 ± 0.65***	5.58***	(+)			0.37 ± 0.09***	(+)	(+)	
Carduelis cannabina	Common linnet	−12.53 ± 2.04***	3.09***	(−)			0.16 ± 0.06**	(+)	4.07 ± 0.69***	
Coturnix	European quail	−7.76 ± 7.67	2.41***	(−)	(−)	(−)			(+)	
Emberiza calandra	Corn bunting	−15.54 ± 4.48***	6.78***	(−)	−5.06 ± 1.86**	−4.17 ± 1.93*	(+)	0.51 ± 0.22*	5.81 ± 1.43***	
Emberiza cia	Rock bunting	−7.05 ± 1.03***	2.39*	0.43 ± 0.13**			(+)	(+)	0.75 ± 0.33*	
Emberiza hortulana	Ortolan bunting	−14.05 ± 2.17***	4.38***	0.75 ± 0.31*			0.44 ± 0.17**	(+)	1.61 ± 0.56**	
Falco tinnunculus	Common kestrel	−8.91 ± 2.26***		(−)	(+)	(+)	0.25 ± 0.12*		1.3 ± 0.59*	
Galerida cristata	Crested lark	−1.29 ± 4.37	1.01*	−0.49 ± 0.25*	−5.14 ± 1.31***	−4.96 ± 1.36***	(+)	(−)	(+)	
Galerida theklae	Thekla's lark	−7.49 ± 5.92	1.64	−0.98 ± 0.15***	(−)	(+)	0.3 ± 0.09**	0.46 ± 0.12***	(+)	
Lanius meridionalis	Iberian grey shrike	−9.04 ± 0.81***	2.26**							
Lanius senator	Woodchat shrike	−12.37 ± 14.36	3.49***	(+)	−1.47 ± 0.73*	(−)	−0.24 ± 0.07***	(+)	(+)	
Lullula arborea	Woodlark	−14.25 ± 4.65**	3.97**	(−)	(−)	(−)	(−)	(−)	5.18 ± 1.65**	
Oenanthe hispanica	Western black-eared wheatear	−15.43 ± 3.64***	2.44*	−0.66 ± 0.13***			0.24 ± 0.07**	(+)	5.73 ± 1.29***	
Oenanthe leucura	Black wheatear	−23.09 ± 5.79***		(+)			(+)	(+)	6.96 ± 2.22**	
Petronia	Rock sparrow	−11.63 ± 4.54*	1.0***	(+)	−3.11 ± 1.42*	−2.94 ± 1.48*	(+)	(+)	3.52 ± 1.71*	
Phoenicurus ochruros	Black redstart	−10.87 ± 13.29	1.01*				(+)	(−)	(+)	
Saxicola torquata	European stonechat	−8.34 ± 4.66	4.97***	0.27 ± 0.1**	(+)	(+)	0.27 ± 0.06***	(−)	(+)	
Upupa epops	Eurasian hoopoe	−5.15 ± 6.38		(−)	−2.98 ± 0.57***	−2.3 ± 0.6***	−0.26 ± 0.09**	(+)	(+)	

The table shows the model parameter coefficient, its standard error (±SE) and the associated *p*-values:
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

subsequent growth and persistence of populations (Donner et al., 2010; Jackson and Sax, 2010). Propagule dispersal is influenced by the density, proximity and productivity of source populations, as well as by dispersal mechanisms, in particular, those that most influence long-distance dispersal (Kinlan and Hastings, 2005). After a disturbance, several factors affect the colonization and persistence of open-habitat birds, including species' biogeographical preferences (Devictor et al., 2008a), their colonization ability (Brotons et al., 2005; Fristoe et al., 2017; Gaston and Blackburn, 2002; Webb et al., 2007), the pre- and post-disturbance habitat (Menz et al., 2009; Pons and Bas, 2005; Pons and Prodon, 1996), the size of the disturbed area (Brotons et al., 2008; Crooks et al., 2001; Pons and Bas, 2005), the connectivity between perturbed areas and population sources (Crooks et al., 2001; Drever et al., 2006), and, finally, the landscape context (Bradstock et al., 2005; Ram et al., 2020; Żmihorski et al., 2016).

The habitat created by disturbances may become unsuitable for open-habitat specialists due to plant regrowth and plant succession (Pons et al., 2012; Pons and Prodon, 1996; Ram et al., 2020; Sirami et al., 2007). Post-disturbance plant regeneration is affected by several factors, among which the lack of water stands out (Verdú et al., 2000). This can affect vegetation successional processes (Zavala et al., 2000) thereby influencing the presence and distribution of birds after a disturbance. Rainfall seems to be a major driver of fire occurrence (Beale et al., 2018) and recent global upsurges in wildfire occurrence may signal weather-induced pyrogeographic shifts (Jolly et al., 2015). Geographical dryness gradients therefore will determine the vegetation structure, affect wildfire occurrence (Kutiel et al., 2000; Piñol et al., 1998) and influence the dynamics of open-habitat species and their persistence after disturbance.

Here we analyse colonization patterns in 22 open-habitat bird species in 68 burnt areas in Catalonia using data from 11 years of surveying, and explore the underlying factors in bird species colonization patterns and time-window of occurrence after fire. Three main hypotheses are tested. (1) Drier burnt areas will maintain open-habitat birds for longer periods than wetter burnt areas because of the association of rainfall with plant regeneration. Thus, we expect to find more open-habitat

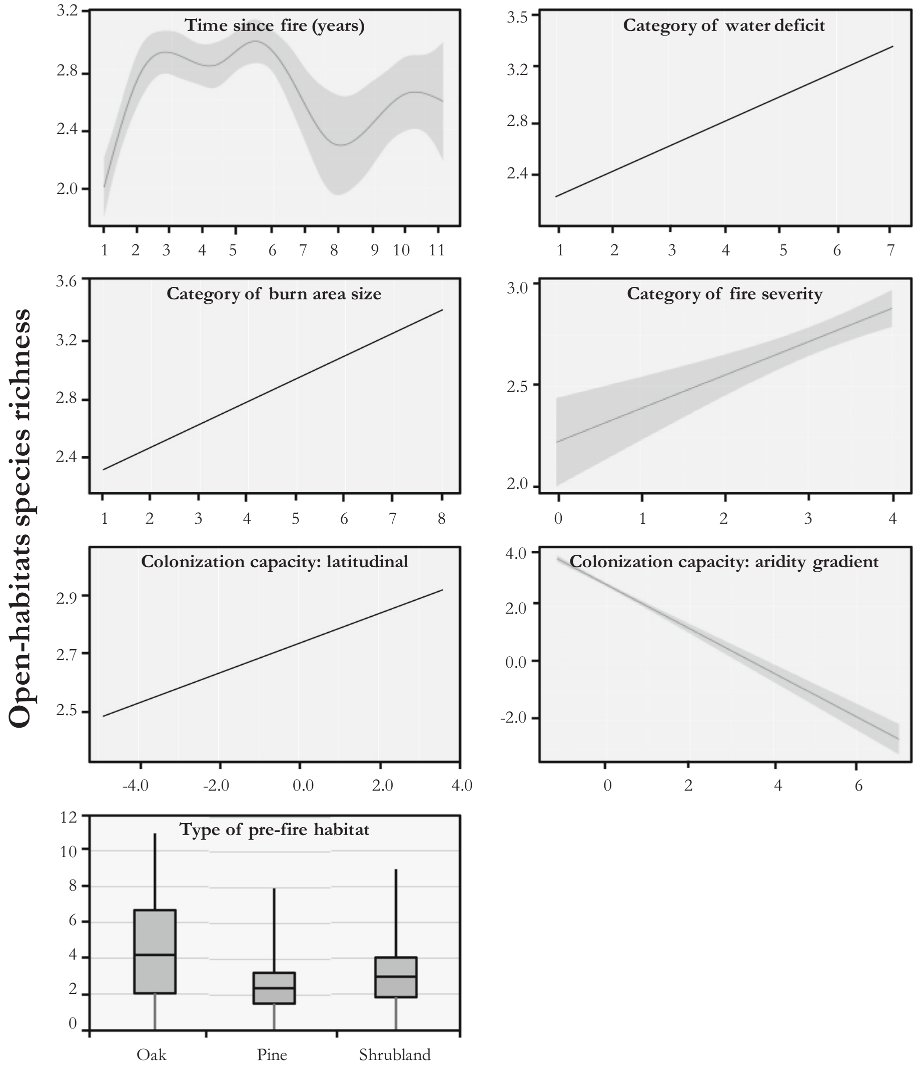

Fig. 2. Model predictions of open-habitat species richness.
Marginal effects (measuring instantaneous rate of change) of the model predictors on open-habitat species richness according to each fixed factor analysed and selected from final model. Trend line and shaded standard error (95 % confidence intervals) were obtained from GAMM model estimates. Lines without shaded areas indicate non-significant relationships. Standard error bars are shown for the type of pre-fire habitat.

species in dry burnt areas that take longer for cover to regenerate. (2) Well-connected burnt areas will allow a greater dispersal from the sources of colonization, therefore facilitating greater rates of occurrence of individual bird species and increased species richness compared to poorly-connected areas (i.e. the assembly of bird species that are being studied). Here, we predict that the greatest number of species will appear in areas where potential local colonization sources are closest to the disturbed sites. (3) Fire severity will benefit open-habitat colonization and time-window of occurrence, because of a stronger reduction of plant cover in more severe fires. We expect that open-habitat species will preferentially occupy the most severely burnt areas.

2. Material and methods

2.1. Study region

The study was conducted in Catalonia (NE Iberian Peninsula; Fig. 1), a region of some 32,100 km^2 with great environmental heterogeneity due to its steep climatic and topographical gradients. Most of the study area has a Mediterranean climate (Piñol et al., 1998); aridity increases from north to south due to latitude and topography, and from east to west due to continentality. In the Mediterranean basin, human presence since pre-historical times has led to large-scale changes over time in the composition of plant species and the distribution of dominant species. Nowadays, land cover in Catalonia chiefly consists of forests (31 %), evergreen shrublands (29 %) and agricultural land (33 %) (Vallecillo et al., 2013). Fire is a major disturbance process in the region, with about 25 % of the wildland area having been burnt since 1975 (González and Pukkala, 2007). In addition, the land abandonment affecting the northern Mediterranean basin has led to extensive woody plant encroachment and to a greater surface area being affected by wildfires in recent years (Duane et al., 2021). Finally, more extreme meteorological conditions promoted by global warming have given rise to fires of unprecedented intensity (Pausas and Fernández-Muñoz, 2012).

2.2. Sampling design

We studied birds in 68 burnt areas distributed throughout Catalonia ranging in size from 51 to 6647 ha that were affected by wildfires in 2000–2011. The majority (70 %) of burnt areas have moderate water deficit and are located in lowlands or mountains with a Mediterranean climate (Puig-Gironès et al., 2017). Within each fire perimeter we established 500-m long and 200-m wide transects, in which birds were censused once a year over a period ranging from one to 9 years (Fig. 1). The minimum distance between two transects was 150 m and the minimum distance between transects and the edge of the fire-affected area was 50 m. However, the majority of transects were at >100 m from the perimeter. Even when a transect was 50-100 m from the perimeter, it was only one end of the transect that was affected. Observers were trained to mark observations of birds seen or heard outside the burnt

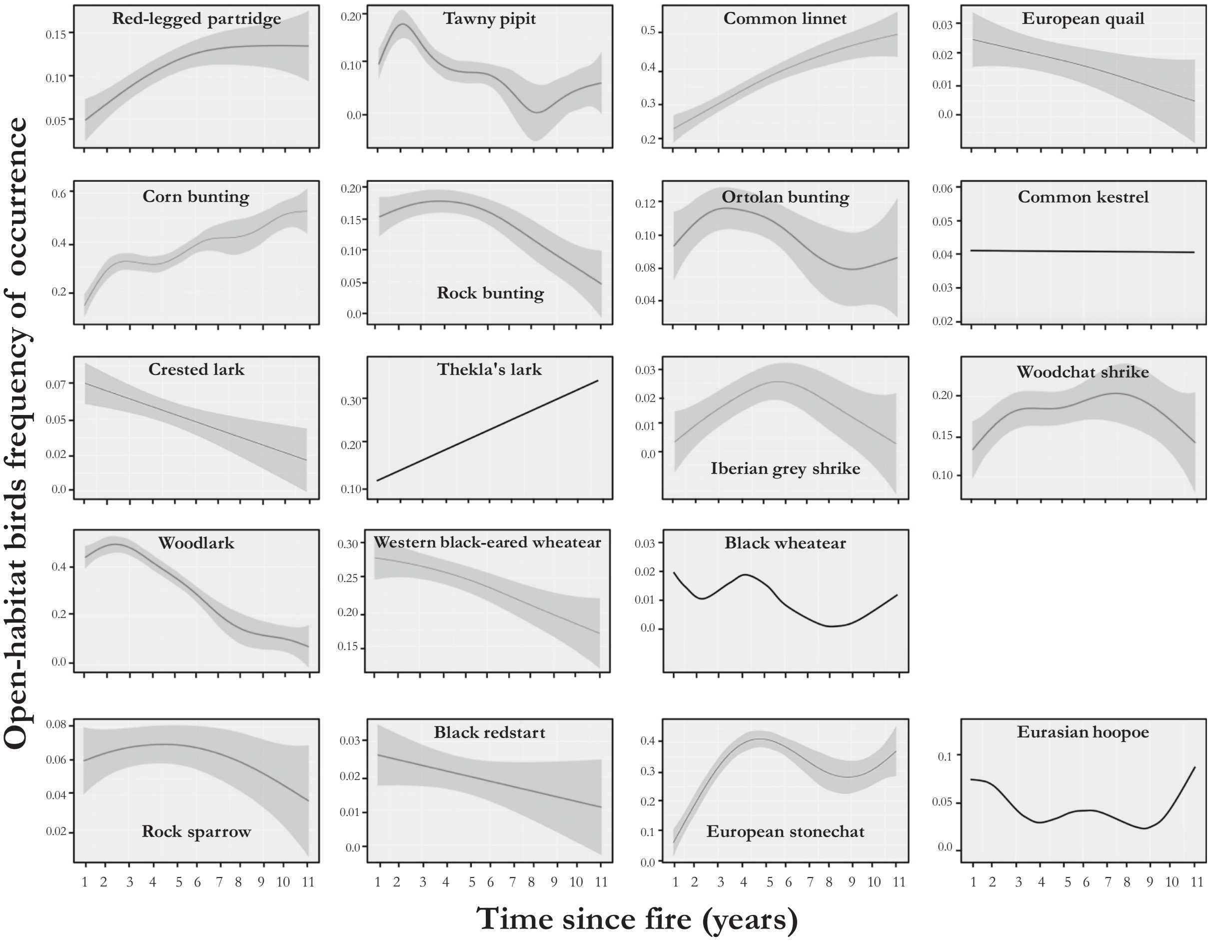

Fig. 3. Model predictions of open-habitat species occurrence over time.
The influence of time since fire on open-habitat species occurrence. Trend lines and shaded standard errors (95 % confidence intervals) were obtained from GAMM model estimates. Lines without shaded areas indicate non-significant relationships.

area and this data (<1 %) were excluded from analyses. The number of transects depended on the size of each burnt area and ranged from two to 41 per burnt area, giving a total of 685. Our database includes the results of 3048 bird censuses conducted in these 685 transects. Each survey was divided into three five-minute periods (15 min in total) and covered around 165 m in length. Birds were counted if heard or seen and were allocated into one of three distance bands (0–25 m, 25–50 m or 50–100 m). Surveys were conducted once during every breeding season (from 10 May to 15 June) in good weather conditions (i.e. without rain or strong wind) during the first 3 h after sunrise by experienced ornithologists walking at a speed of about 2 km per hour (Bibby et al., 2000). The criterion for establishing the number of transects and the sampling protocol is fully explained in Zozaya et al. (2010).

2.3. *Bird data*

Open-habitat birds can be used as indicators of open vegetation structures (Herrando et al., 2016) and allow for comparisons of colonization rates and maximum occurrence due to open-habitat creation by fire. Open-habitat and steppe specialists were defined as those generally occurring in drylands, rocky areas, grasslands, cropland or steppes in the Mediterranean region (Estrada et al., 2004; Herrando et al., 2016; Prodon and Lebreton, 1981). Ecotone, edge and shrubland specialists were not included. The open-habitat bird frequency of occurrence (number of presences/number of surveys, ranging from 0 to 1) per transect was used as a measure of species' relative abundance. <1 % of birds were detected in unburnt surrounding areas and were excluded from the analyses. We focused on the frequency of occurrence of species that inhabit Mediterranean open-habitats and occurred in a minimum of 15 % of the censused burnt areas (Table S1). We excluded from the 25 initial candidates typical but nevertheless rare open-habitat birds such as Eurasian skylark (*Alauda arvensis* L.), Mediterranean short-toed lark (*Calandrella rufescens* Vieillot), yellowhammer (*Emberiza citrinella* L.), red-backed shrike (*Lanius collurio* L.), European calandra-lark (*Melanocorypha calandra* L.) and northern wheatear (*Oenanthe oenanthe* L.).

2.4. *Environmental variables*

Environmental variables were recorded at two different scales: for burnt areas (time since fire, burnt patch size and pre-fire habitat) and transects (water deficit, population proximity index and fire severity). The time since fire (TSF) was measured as the number of years elapsed since the fire (first spring = 1 and so on), and ranged from 1 to 11. In our study area, fires mainly occur in summer (June, July, August and September), and sampling was never carried out in the first 6 months after the fire, i.e., TSF = 1 means that 7 to 13 months have elapsed since the fire. Burnt patch size was defined as the extent of the burnt area (ha) derived from digital maps from the Catalan Government, and was categorized into eight categories (1 = 50–250 ha; 2 = 250–500; 3 = 500–750; 4 = 750–1000; 5 = 1000–1250; 6 = 1250–1500; 7 = 1500–2000; 8 = >2000 ha). Pre-fire habitat consisted of three categorical variables, namely shrubland, pine forest and oak forest, that describe the presence or absence (1/0) of burnt vegetation types along the transect.

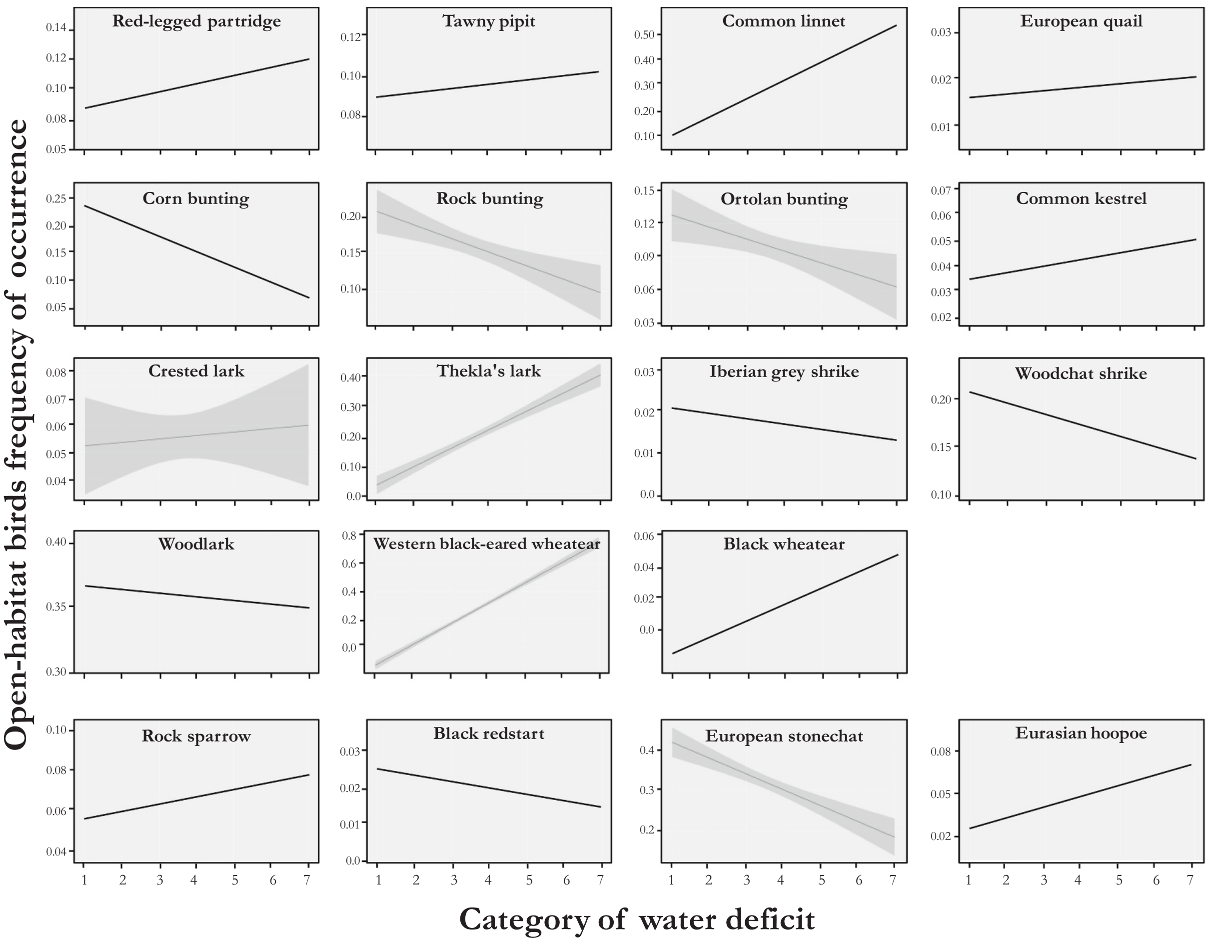

Fig. 4. Model predictions of open-habitat species occurrence over water deficit.
The influence of the gradient of water deficit (from humid (WD1) to dry (WD7) categories) on the distribution of open-habitat species occurrence. Trend line and shaded standard error (95 % confidence intervals) were obtained from GAMM model estimates. Lines without shaded areas indicate non-significant relationships.

Water deficit (WD) as a measure of aridity (both terms are used hereafter interchangeably) was calculated for each transect per year (June–May) using the potential evapotranspiration (PET) and real evapotranspiration (ETr) taken from the Digital Climate Atlas for the Iberian Peninsula (Ninyerola et al., 2003), a 180-m-resolution digital elevation model that uses data from meteorological stations (one station per 64 km^2). We used the equation established by Thornthwaite (Black, 2007; Thornthwaite, 1948) – WD = PET – ETr – that gave values of between −137.9 and 538.3 mm for our transects. To graphically represent the effect of aridity on open-habitat birds, the water deficit was divided into categories of 100 mm each, in which the first category (WD01) corresponds to transects with values from 0 to negative values, while WD07 represents the groups with values in the range 500–600 mm.

The population proximity index for each species and transect was calculated using presence-absence data taken from the Catalan Breeding Bird Atlas (Estrada et al., 2004). We considered three buffers based on 10 × 10-km buffers: the first corresponded to the buffer in which the focal transect was located, the second to the eight neighbouring buffers, and the third to the 16 buffers surrounding the second group (Fig. 1). Each of the three buffer areas had a value of 0–1, thereby giving an index between 0 (absence of the focal species from all squares) and 3 (presence in all 25 squares). The value of each buffer gives most weight (1 point) to the square including the focal transect, an intermediate weight to the closest squares (1/8 points per square), and least weight to the most distant squares (1/16 points per square), which reflects the distance-dependent colonization of burnt areas (Brotons et al., 2005). Finally, the burn severity index of the transects was calculated using an ordinal variable at four points (Fig. 1) with values ranging from 0 (many unburnt patches throughout the transect area) to 4 (the area surveyed along transect had been completely burnt by a severe fire).

2.5. Data analyses

First, we used Generalized linear mixed models (GLMMs), with Poisson error structure and log link function, including the interaction between time since fire and water deficit, to assess whether aridity influences temporal patterns of open-habitat species richness and individual species occurrences. Secondly, Generalized additive mixed models (GAMM), with Poisson error structure and log link function, were used to analyse the effects of time since fire, pre-fire habitat, burnt patch size, water deficit, population proximity index, and the burn severity index on open-habitat bird species richness. The community population proximity index value was extracted from the proximity index for each species-transect population, as explained in the previous paragraph, using a principal component analysis (PCA; Fig. S1). The first principal component (0.32 proportion of variance), hereafter 'latitudinal effects', showed a clear latitudinal gradient, in which lower scores occurred primarily in southern burnt areas, with hotter temperatures, and higher scores in northern burnt areas with cooler temperatures. The second component (0.22 proportion of variance), hereafter 'aridity effects', reflects the gradient from wet to arid transects. Transects, nested within locality, were included as a random factor to control for possible site-based differences. The frequency of occurrence (0 to 1)

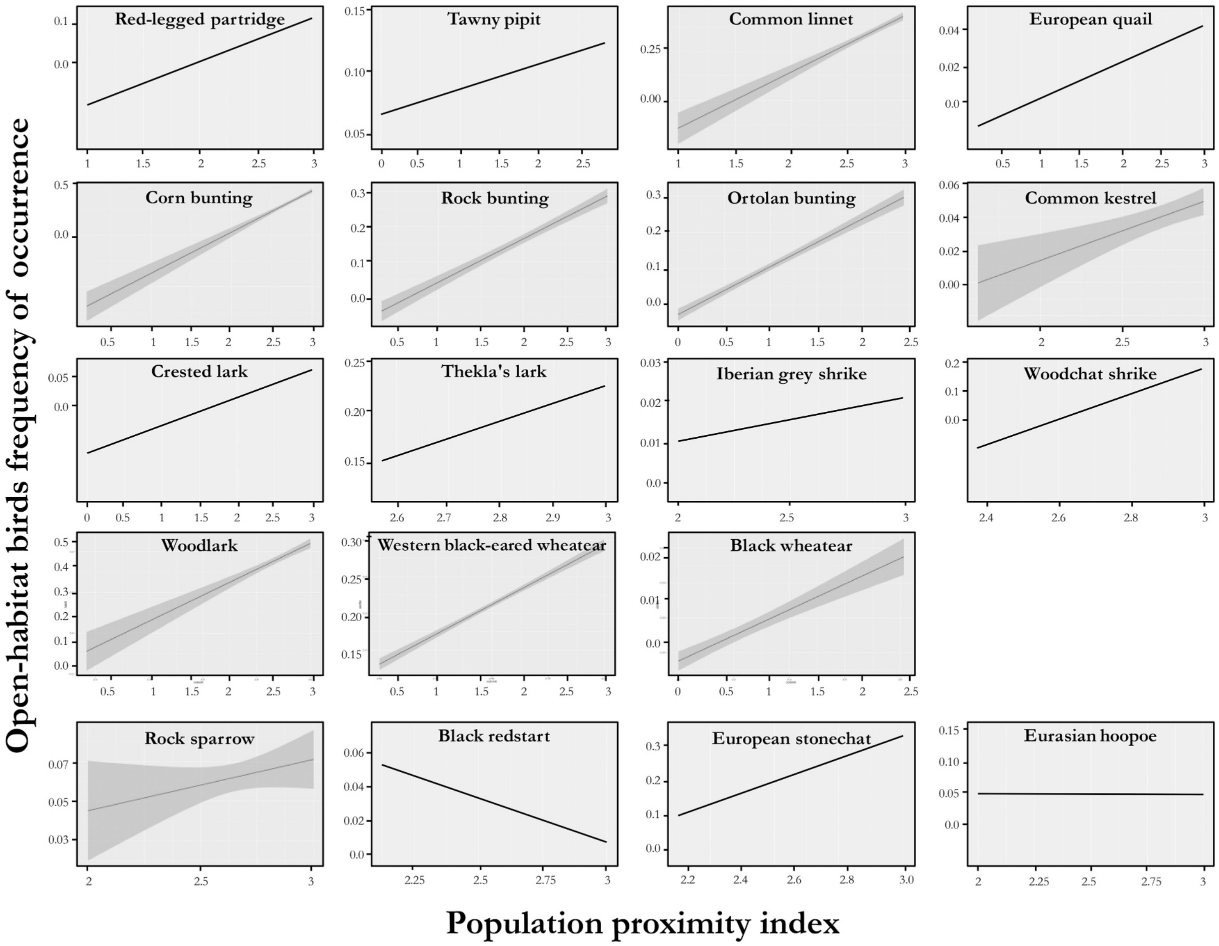

Fig. 5. Model predictions of open-habitat species occurrence over population proximity index.
The influence of the population proximity index on the distribution of open-habitat species occurrence. Trend line and shaded standard error (95 % confidence intervals) were obtained from GAMM model estimates. Lines without shaded areas indicate non-significant relationships.

in censuses for each open-habitat bird was used since it provides a better comparison between species than relative abundance, and minimizes existing differences in detectability. Generalized additive mixed models (GAMM) with a binomial error structure and log link function were used to analyse the influence of time since fire, pre-fire habitat, burnt patch size, water deficit, population proximity index and burn severity index on the relative abundances of open-habitat species. GAMM are a powerful and flexible way of performing regression analyses (Wood, 2017), and consist of Generalized Lineal Mixed Models (GLMM) with smoothed splines fitted to the explanatory variables rather than to the original values of the variables. Time since fire and water deficit were treated as smoothed variables, and all other variables were included as linear terms.

We used a multi-model inference approach to select the most important variables in the GAMM. This approach is based on all possible submodels developed from a set of explanatory variables, which restricts model selection bias and provides a relative measure of each predictor's importance (weight of evidence). All possible models were ranked according to their Akaike Information Criteria corrected for small samples (AICc) (Burnham and Anderson, 2002) and followed a series of hierarchical steps. (1) The diagnostic plots of fitted values, residuals and the fitted splines were analysed for each term of each model to assess the goodness of fits. (2) Multicollinearity diagnostics were performed by quantifying generalized variance-inflation factors (GVIF) calculated for each fixed factor (Fox and Monette, 1992), where large GVIF values (arbitrary threshold of $\leq$2.5 suggesting collinearity) were sequentially dropped from further analysis (Zuur et al., 2010). (3) For each model, the AIC weight (AICω) was calculated (AICω sum for all models is equal to 1) (Wagenmakers and Farrell, 2004). (4) Furthermore, if there was no clear most parsimonious model (one or more models with a difference in AIC of less than two from the best model), the average final model was estimated from all of these models (Burnham and Anderson, 2002). (5) To interpret the magnitude of each variable on the average final model, the relative importance of each variable (RVI) was weighted based on the sum of ωi for each variable (Table S2). The RIV ranged from 0 to 1, so that the explanatory variable was considered robust if it had an RIV > 0.9; a moderate effect between 0.6 and 0.9; a weak effect between 0.5 and 0.6; and no effect below 0.5 (Chiaradia et al., 2016; Kennedy et al., 2013). (6) Furthermore, if standard errors (SE) were large (1.96 * SE > parameter appreciation, for the 95 % confidence intervals) the estimate of the parameter was considered imprecise. To perform these analyses, R software (R Development Core Team, 2017) with the *gamm4* (Wood and Scheipl, 2014), *lme4* (Bates et al., 2015), *car* (Fox and Weisberg, 2011), *MuMIn* (Bartoń, 2016) and *ggplot2* (Wickham, 2009) packages were used. Finally, the model-predicted post-fire responses of birds were classified into categories following Watson et al. (2012).

3. Results

During the study, 8345 detections of 22 open-habitat bird species were obtained. Individual transects harboured 0–10 open-habitat species (mean = 2.7). Our explanatory GLMM combining time and water deficit indicated than the interaction between both variables did not affect species richness of open-habitat birds (Table 1). On the other

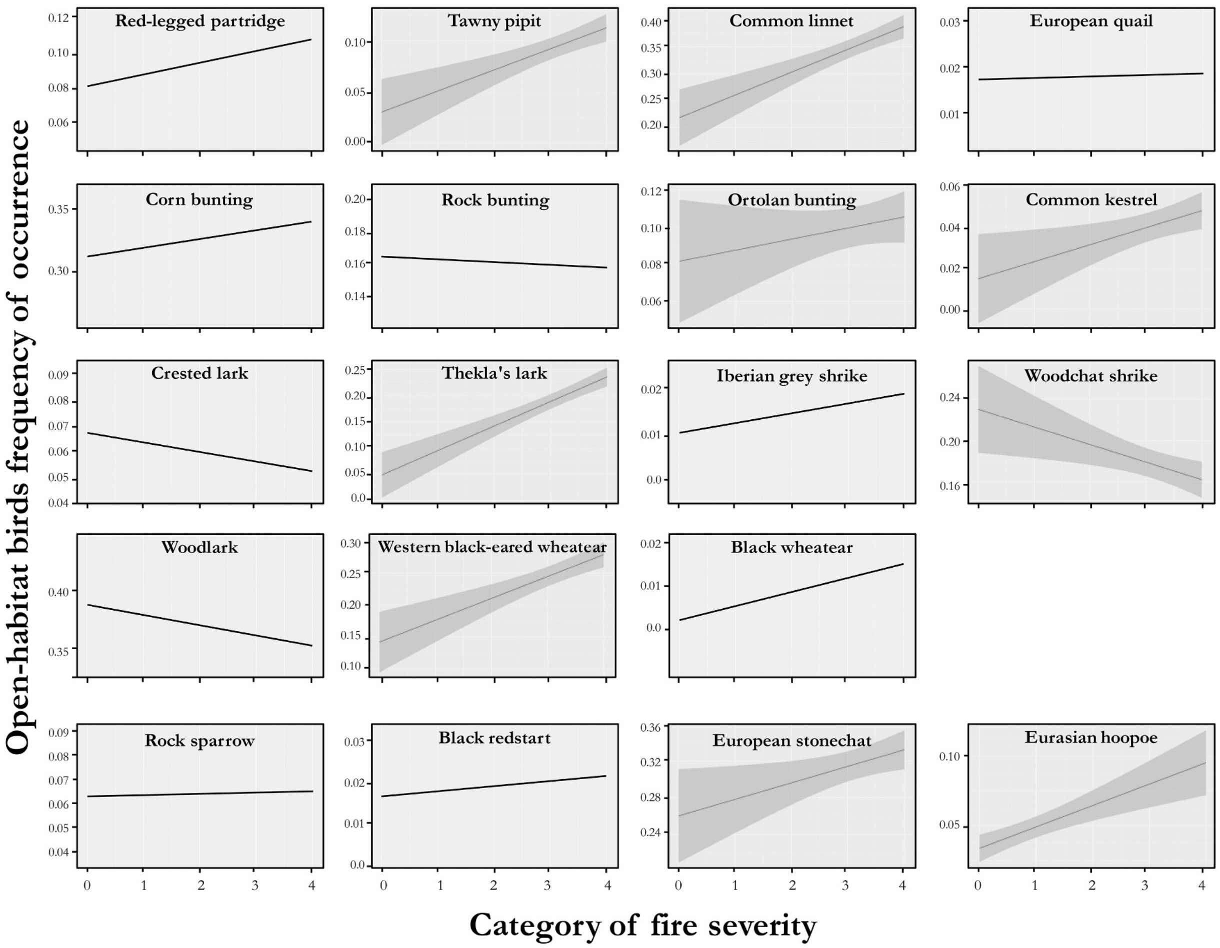

Fig. 6. Model predictions of open-habitat species occurrence over fire severity.
The influence of the category of the fire severity on the distribution of open-habitat species occurrence. Trend line and shaded standard error (95 % confidence intervals) were obtained from GAMM model estimates. Lines without shaded areas indicate non-significant relationships.

hand, the GAMM showed that open-habitat species richness had a significant relationship with both time since fire, and fire severity, but had a negative relationship with the aridity effects component derived from the PCA (Table 2). Open-habitat species richness, which was positively associated with time since fire, sharply increased during the first 3 years after the fire but then decreased more slowly (Fig. 2). The size of the burnt areas and pre-fire habitat had a non-significant effect (Table 2).

The most common species (occurring in >30 % of locations) were the red-legged partridge (*Alectoris rufa* L.), common linnet (*Carduelis cannabina* L.), woodchat shrike (*Lanius senator* L.), woodlark (*Lullula arborea* L.) and European stonechat (*Saxicola torquata* L.), while common linnet, corn bunting (*Emberiza calandra* L.), woodlark, Western black-eared wheatear (*Oenanthe hispanica* L.) and European stonechat had the highest frequency of occurrence. From the 19 open-habitat species, five showed effects of the time and water deficit interaction (Table 1), two decreased their occurrence in arid zones over time and three increased their occurrence. However, GAMMs analysis showed than fifteen species were significantly related to time since fire (Fig. 3) and six species to water deficit (Fig. 4). Different types of curves representing diverse temporal post-fire responses in the open-habitat bird were found, including decline (6 species), incline (3), irruptive (4), bell (2), plateau (2) and null (2) (Fig. 3). The colonization of transects was also positively associated with their colonization potential, which was measured based on the occurrence of species in neighbouring squares and the proximity to population sources (significant effect in nine species; Fig. 5), and with fire severity (nine species; Fig. 6). Larger burnt areas had a greater probability of being colonized or remaining occupied by open-habitat species, however, only five species show a significant relationship between their frequency of occurrence and this variable in the final models (Table 2). Finally, pre-fire habitat was significant for the frequency of occurrence in five bird species (Fig. 7).

4. Discussion

In this study, we examined how open-habitat bird species colonize burnt areas and how their occurrence changes over time, and also studied correlates of open-habitat species richness in recently burnt areas. Open-habitat bird species occurrence depended mainly on time since fire, water deficit, fire severity and population proximity, the latter calculated for each species as the relative distance between population sources and individual burnt areas. Our results also support previous findings on the key role than fire plays in the distribution dynamics of open-habitat species in the Mediterranean (Brotons et al., 2005; Puig-Gironès et al., 2018; Rollan and Real, 2011; Santos et al., 2009; Santos and Poquet, 2010; Zozaya et al., 2012), especially in areas of high aridity and/or high fire severity that therefore have less plant cover (Puig-Gironès et al., 2017).

The dynamics of bird species colonization and local extinctions are mainly the result of successional changes in habitat conditions, as found in previous studies (see e.g. Fox (1982) or Jacquet and Prodon (2009)). Species turnover mainly consists in the early post-fire occurrence of bare-ground specialists (Fox, 1982; Pons and Prodon, 1996), followed by species that require herbaceous undergrowth, and their progressive replacement by species tolerant to the growth of the shrub layer along

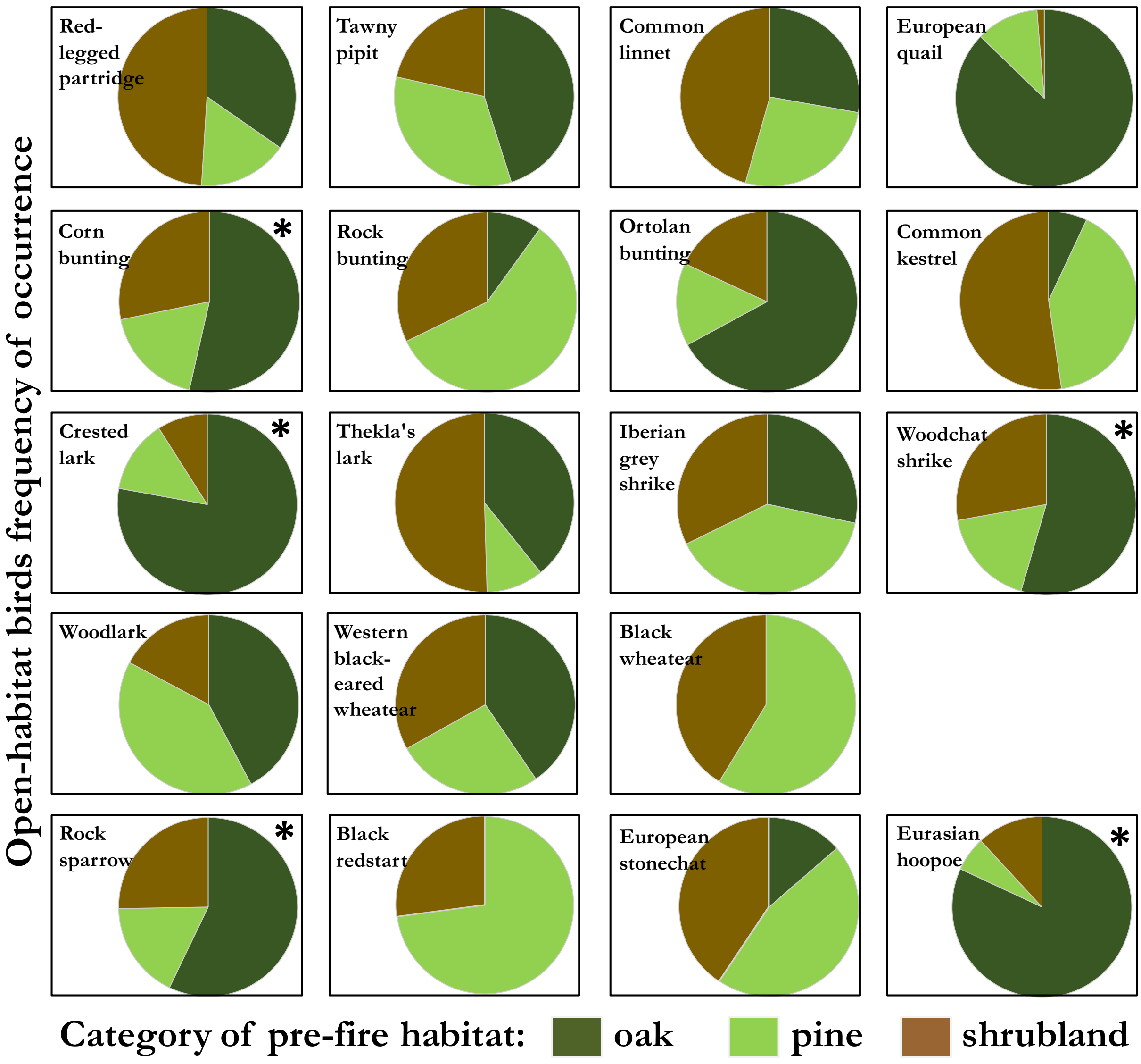

Fig. 7. Representation of open-habitat species occurrence over pre-fire habitat.
We show the influence of the category of the pre-fire habitat (oak, pine or shrubland) on the distribution of open-habitat species occurrence after fire. The asterisk means that the pre-fire habitat variable is significantly present in the final model presented in Table 2.

succession (Puig-Gironès et al., 2017). Colonization takes place more quickly than species disappearances, which may not have been detected in the relatively short time period (11 years) of the study (Brommer et al., 2012; Mason et al., 2019). Bird species can however show time lags in the colonization of burnt areas due to dispersal and establishment constraints (Brotons et al., 2005). In addition, open-habitat birds found in burnt areas may exhibit site tenacity and, even if the habitat is no longer optimal, birds may persist longer than expected due to behavioral mechanisms such as territoriality, although this should be demonstrated using a capture-recapture study. Examples of site tenacity may include the time persistence we found in the ortolan bunting, tawny pipit, European quail and woodlark.

Different species peak at different time since fire, due to changes in the availability of resources as time after disturbances progresses (Hutto, 2008; Smith et al., 2013). But population peak time can be affected by an increase in aridity or by the exploitation of burnt forests. Aridity has a severe effect on post-fire vegetation recovery in the Mediterranean basin (Puig-Gironès et al., 2017), and a significant influence for rock bunting, ortolan bunting, crested lark, thekla's lark, Western black-eared wheatear and European stonechat. Climate change will likely increase water deficit and lead to greater water stress for Mediterranean vegetation (Kutiel et al., 2000). A geographical aridity gradient, as was studied here, can act as a proxy for evaluating the pressure that animals experience with increasing water deficit. Accordingly, water deficit plays an important role in the presence and stability of open-habitat species. Indeed, some species select warm dry sites and benefit from drier conditions, because these sites keep appropriate vegetation structure longer than the more mesic sites (Puig-Gironès et al., 2017). However, increased aridity can also negatively affect arid land bird communities due to food limitations derived from water constraints (Roberts et al., 2021). Wood harvesting may also benefit declining bird species if salvage logging takes place (Rost et al., 2012). However, forests tend to be associated with more productive sites (Thuiller et al., 2003), with faster vegetation recovery shortening the time-window in which these areas hold suitable open habitats.

Our results also suggest that open-habitat birds are more frequently detected in burnt areas near previously occupied areas, which supports previous findings (Brotons et al., 2005). Distance-limited colonization greatly influences the future composition of a bird community in a given region. Even though a few studies have suggested long-distance dispersal by open-habitat species such as ortolan bunting (Dale et al., 2005), dispersal capabilities may generally – and critically – constrain the effective colonization of distant suitable areas (Brotons et al., 2008). On the other hand, generalist species are known to have better colonizing abilities and to cope better with disturbances (Devictor et al., 2008b). Species tolerant to habitat fragmentation also detect and colonize new habitat faster than more sensitive species (Villard and Taylor, 1994). The occurrence of open-habitat species seems therefore to be determined by interactions between geographical isolation (less interaction and lower connectivity) and the landscape matrix (non-suitable habitat surrounding habitat patches) (Vögeli et al., 2010). In this sense, the effects of the landscape matrix configuration on open-habitat bird assemblages should be assessed in the future.

Our findings also underscore the importance of fire severity for the colonization and persistence of open-habitat bird species, as well as the benefits of more severe fires for species with unfavourable European conservation status. Open-habitat birds positively react to structural changes in vegetation induced by fires in the Mediterranean basin (Brotons et al., 2005; Pons and Bas, 2005; Pons and Prodon, 1996). The magnitude of change in vegetation variables derived from fire increases with fire severity (Smucker et al., 2005) and entails significant changes in bird-species richness and abundance according to the habitat preferences of the species in question (open, shrub or forest) and the location of the burnt area (Hutto and Patterson, 2016; Lindenmayer et al., 2014; Pons and Clavero, 2010; Smucker et al., 2005). Similarly, other natural and anthropogenic disturbances in forest allow farmland birds to colonize recently opened areas (Kamp et al., 2020; Ram et al., 2020; Thorn et al., 2016; Żmihorski et al., 2016). Finally, our data also reveals that over time larger burnt areas have greater probabilities of being colonized or remaining occupied by open-habitat birds. Nevertheless, few species have a significant relationship with burnt-area size in the final models. We thus believe that size may be related to certain factors that were not taken into account, such as whether or not a species is prone to colonize, the connectivity between disturbed areas and population sources, and its possible positive correlation with fire severity.

4.1. Conservation implications

Our results show how open-habitat species richness rapidly reached maximum after fire disturbance. This happened between two and 6 years after fire in the study region. Previous work suggests that this post-fire time window is appropriate for open habitat species in the Western Mediterranean basin (Jacquet and Prodon, 2009). However, not all studied species preferred this post-fire age interval, because some were more abundant later on. In the study region, the mean fire return interval is >60 years (Duane and Brotons, 2018). Mid-successional vegetation (older than 6 years after fire) covers important areas and the habitat requirements of species that prefer >6-year-old vegetation is usually met at a landscape scale. Therefore, avoiding local extinctions of early successional species should be prioritized, given their conservation status. These species are also the most sensitive to fire regime changes (Zozaya et al., 2012). Integrated fire management can help generating a landscape matrix with patches of different fire ages, to preserve a rich open-habitat bird community and avoid local extinctions (see e.g. Kelly and Brotons (2017) or Beale et al. (2018)). Our results showing the greater value of high severity fires, may indicate that wildfires are likely to be more beneficial than prescribed burns, which are generally of lower severity. This can be a challenge to the effective use of burning to create an appropriate mix of post-fire successional stages across the landscape. A connectivity between source populations and the new patches is required to facilitate species dispersal. To this aim, the distance between old and new patches should be kept to <5 km to favour most species, as other authors suggested (Brotons et al., 2005). The tools for such a focused landscape management include repeated prescribed fires and livestock/wildlife grazing that maintains vegetation in early successional stages that can host open-habitat bird populations (Pons et al., 2003; Virgós et al., 2003). High-intensity burning with high tree mortality, in particular, can be used as a management tool to increase densities of birds associated with open habitat, although may have adverse effects on shrub-strata associated species (Greenberg et al., 2007). Low severity fires can therefore be applied to previously large burnt areas to generate mosaics and increase bird diversity (Sitters et al., 2015). Depending on specific objectives and environmental conditions, the fire return interval should be 5 to 20 years, as other authors have pointed out (Jacquet and Prodon, 2009). At regional scale, fire history and floristic composition will determine the recovery of grass, shrub and tree layers after a fire. In addition, abiotic factors such as fire severity, precipitation, altitude and topography will also have an important effect on the recovery (Díaz-Delgado et al., 2002; Puig-Gironès et al., 2017). It is also needed to determine the optimal size of burnt patches in managed areas, depending on the conservation objectives.

Climate change scenarios suggest a future increase in aridity and more severe wildfires in the next decades. Our results suggest a positive effect of severe fires on open-habitat species. Therefore, knowledge of the fire severity that favours the presence of threatened species is useful when managing the habitat with prescribed fires. This is required to be able to carry out informed management aimed at favouring particular threatened species in certain sites. To respond to new challenges, the climatic, temporal and environmental drivers that facilitate the colonization and persistence of threatened open-habitat species need to be continuously assessed in light of a rapidly changing nature.

CRediT authorship contribution statement

Roger Puig-Gironès: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Lluís Brotons:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Pere Pons:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109661.

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