Forest Ecology and Management 549 (2023) 121439

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Examining the temporal effects of wildfires on forest birds: Should I stay or should I go?

Roger Puig-Gironès[a,b,*], Lluís Brotons[c,d,e,f], Pere Pons[a], Marc Franch[a,g]

[a] Animal Biology Lab. Departament de Ciències Ambientals, Universitat de Girona, C. Maria Aurèlia Capmany 69, Girona, Catalonia 17003, Spain
[b] Equip de Biologia de la Conservació, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals & Institut de la Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Av. Diagonal 643, Barcelona, Catalonia 08028, Spain
[c] Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Cerdanyola del Vallès, Catalonia, Spain
[d] CSIC, Cerdanyola del Vallès, Spain
[e] CTFC, Solsona, Spain
[f] ICO, Barceona, Spain
[g] CICGE – Centro de Investigação em Ciências Geo-Espaciais, Observatório Astronómico Prof. Manuel de Barros, University of Porto, Vila Nova de Gaia 4430-146, Portugal

ARTICLE INFO

Keywords:
Biological legacies
Fire heterogeneity
Forests birds
Salvage logging
Site fidelity
Water déficit

ABSTRACT

In flammable ecosystems, forest dynamics are affected by fire suppression, climate change and changes in land use that cause the frequency and intensity of fires to diverge from natural fire regimes. Although afforestation provides new habitats for forest species, fire can reverse its benefits by penalizing forest species. Shorter fire recurrence may also affect the capacity of original habitats to recover with post-fire salvage logging adding to the picture and having both direct and indirect effects on birds. To identify the underlying factors driving temporal variations in forest bird populations after wildfires, we performed counts in 685 transects located in 68 burnt areas in Catalonia (NE Iberian Peninsula), ranging from one to 11 years post-fire. Among the 20 studied forest species, 18 related significantly to time since fire and 14 to water deficit. Post-fire bird responses mainly fitted to non-lineal responses, such as irruptive and inverse-irruptive trends; whereas water deficit matched with the inclined and bell-shaped trends. Individual site fidelity seems behind the decision of forest birds to stay or leave after a fire, leading to increase frequency of occurrence immediately after fire but this effect tends to diminish over time. In terms of the spatial characteristics of burnt areas, the majority of species showed a positive relationship with fire severity heterogeneity and the density of unburnt patches. On the other hand, salvage logging negatively affected forest bird diversity. Bird diversity also decreased with the time since fire and in the driest transects but fire heterogeneity was positive for alpha and beta bird forest diversity. The relationships between forest birds and the mosaic of burnt and unburnt areas created by wildfires plays a critical role in maintaining biodiversity in fire-prone ecosystems. Thus, limiting post-fire disturbance (e.g. salvage logging) and promoting natural regeneration could be an effective strategy that will benefit forest organisms such as birds. Maintaining unburnt patches and creating a mosaic of burn severity and vegetation will promote habitat heterogeneity and benefit a diverse range of bird species.

1. Introduction

In flammable ecosystems, variability in burnt areas creates a diversity of ecological niches that become available for species that respond positively to fire. This pyrodiversity is predicted to strongly shape spatial and temporal patterns of biodiversity in areas affected by fire (Tingley et al., 2016; Kelly and Brotons, 2017; Pausas and Parr, 2018). However, the natural processes occurring in forests have been altered in many regions and the frequency and intensity of fires no longer correspond to natural fire regimes as a result of fire suppression, climate change, changes in land use and a combination of all these factors (Cochrane and Barber, 2009; Pausas and Fernández-Muñoz, 2012; Brotons et al., 2013). Consequently, fuel accumulation, which refers to the growth of vegetation and the establishment of new forests

---

* Corresponding autor.
E-mail address: roger.puig.girones@gmail.com (R. Puig-Gironès).

https://doi.org/10.1016/j.foreco.2023.121439
Received 15 June 2023; Received in revised form 13 September 2023; Accepted 15 September 2023
Available online 4 October 2023
0378-1127/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

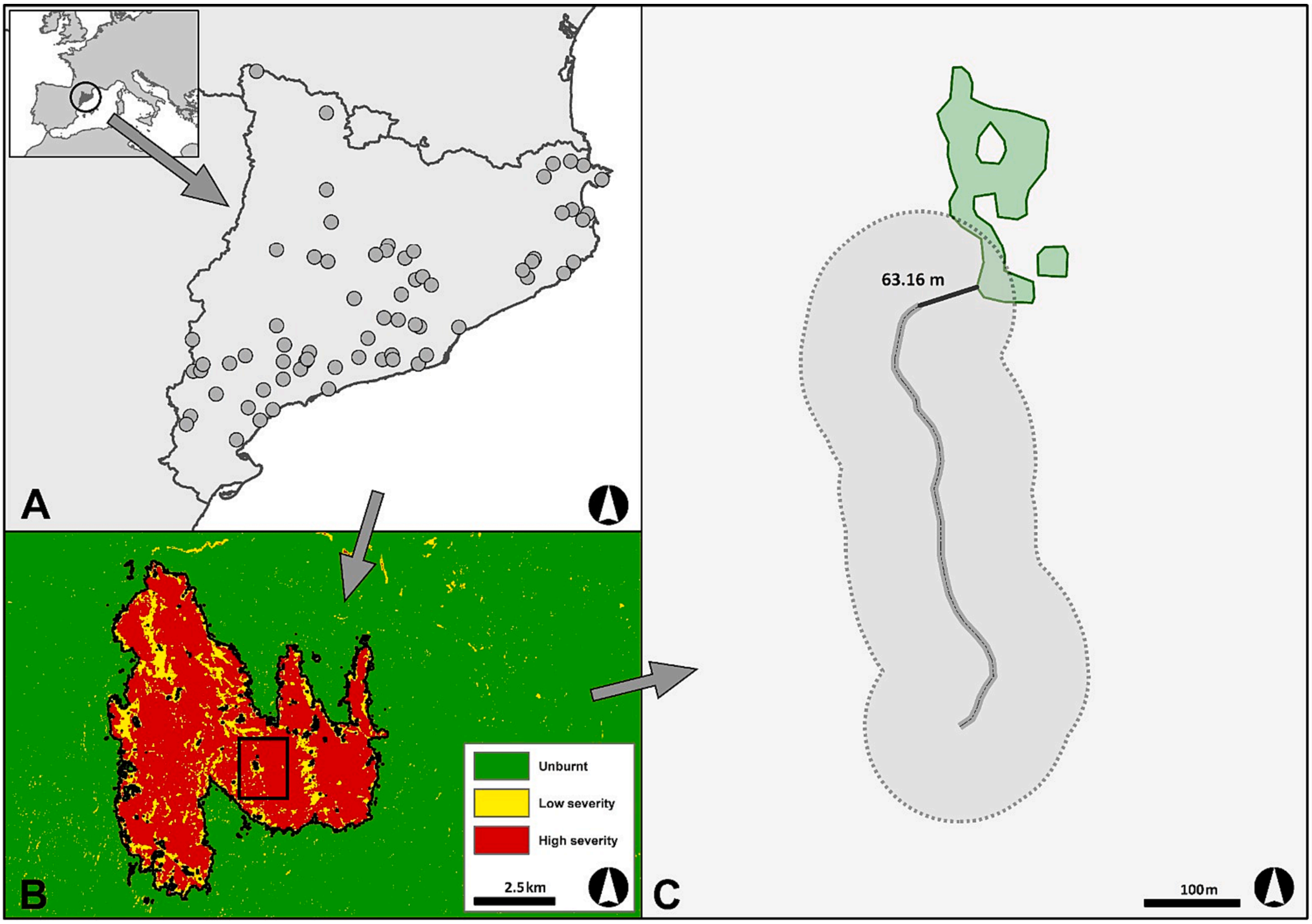

Fig. 1. Site location and sampling design scheme. Spatial distribution (A) of the 68 burnt areas (represented by dark grey points) across Catalonia. Each point indicates the location of a specific burnt area. Assessment of fire severity (B) using the differenced Normalized Burn Ratio (dNBR) in the Sant Llorenç Savall (15BA) burnt area (fire of 10/08/2003). The burnt area encompassed 4,619.75 ha, depicted by the black perimeter. The minimum distance from the burnt patches to unburnt areas (C) along a specific transect within the Sant Llorenç Savall fire zone.

(referred to afforestation), occurs in some forests that lack natural disturbance. This phenomenon is often associated to an increased likelihood of catastrophic fire events (Bowman et al., 2009). Recent surges in the number of wildfires may also signal weather-induced pyrogeographical shifts (Jolly et al. 2015) and rainfall has been identified as major driver of fire recurrence (Beale et al., 2018). Thus, the vegetation structure and wildfire probability will be influenced by gradients of geographical dryness (Piñol et al., 1998; Kutiel et al., 2000).

Afforestation favours the development of late successional stages within landscapes and consequently benefits forest-associated species (Falcucci et al., 2007; Herrando et al., 2016). Forests are important habitats for (i) specialist organisms that are well adapted to forest environments and (ii) generalist species that are able to occupy a variety of habitats (Brunet et al., 2011). Nevertheless, afforestation can also homogenize habitats, thereby having a negative impact on open-habitat species and lead to their progressive isolation and local extinction (Burrascano et al., 2016; Herrando et al., 2016; Franch et al., 2021). Fire usually reverses afforestation by penalizing forest species and benefitting early succession open-habitat species (Moreira and Russo, 2007; Brotons et al., 2008; Puig-Gironès et al., 2023c). Shorter fire recurrence is leading to increased occurrences of young forests types, benefiting early-successional species (Francos et al., 2016; Puig-Gironès et al., 2017), while posing challenges for forest specialists, which may become excluded from this type of landscape (Brunet et al., 2011; Naaf and Kolk, 2015). Deviation from the natural fire recurrence pattern may also affect the capacity of the original habitat structure and composition to recover (Retana et al., 2002) and the resilience of plant communities (Keeley, 1986; Pausas et al., 2004). Water availability, a limiting factor for plant succession (Zavala et al., 2000), may indirectly influence the occurrence of animals such as birds after a wildfire due to their dependence on vegetation structure (Lopez and Moro, 1997; Puig-Gironès et al., 2017; Puig-Gironès et al., 2022).

Salvage logging is a common management practice performed after wildfires that involves removing dead or damaged trees from burnt areas (Lindenmayer and Noss, 2006; Pons and Rost, 2017; Thorn et al., 2018). This additional disturbance can have both direct and indirect effects on birds depending on species traits, fire severity and the type and intensity of the salvage logging operations undertaken (Cahall and Hayes, 2009; Saab et al., 2009; Rost et al., 2013; Georgiev et al., 2020). Consequently, salvage logging is likely to have a significant impact on bird diversity and reduce the alpha diversity (the number of species present in each area and their abundances) by removing habitat features such as snags, cavities and natural regeneration. It also has the potential to alter the relative species composition between areas, thereby affecting between-site diversity (β-diversity) (Cahall and Hayes, 2009; Saab et al., 2009; Thorn et al., 2020). Additionally, the habitats resulting from fire and logging may tend to disrupt bird behaviour as birds are known to be strongly territorial during breeding (Nice, 1941) and exhibit site fidelity or tenacity, i.e. their tendency to return to known areas for breeding, nesting and/or foraging (Emlen, 1970; Greenwood, 1980). Thus, after fires, birds may either abandon the disturbed habitat or remain in it (Pons et al., 2003), so the presence of a given species will not be directly

Table 1

Forest bird species. List of forest bird species censused in the 685 transects located in 68 burnt areas in Catalonia. For each species the scientific and common name, the abbreviation, its migratory behaviour, the local distribution, the habitat preferences, the number of burnt areas where it is present (from a total of 68) and the number of transects where it has been found (from a total of 685, censused one to nine years) are shown. The highlighted species have low numbers, making them unsuitable for individual analyses.

Common name	Scientific name	Abbreviation	Migratory behaviour	Local distribution	Habitat preferences	Areas where is present	Transects where is present
Long-tailed tit	Aegithalos caudatus L.	AEGCAU	Sedentary	Extend present	Forests	31	62
Tree pipit	Anthus trivialis L.	ANTTRI	Migrant	Humid areas	Open forests	4	6
Short-toed treecreeper	Certhia brachydactyla Brehm	CERBRA	Sedentary	Extend present	Forests	42	169
Common wood pigeon	Columba palumbus L.	COLPAL	Sedentary	Extend present	Generalist forest	61	344
Common cuckoo	Cuculus canorus L.	CUCCAN	Migrant	Extend present	Generalist forest	44	176
Great spotted woodpecker	Dendrocopos major L.	DENMAJ	Sedentary	Humid areas	Forests	38	141
European robin	Erithacus rubecula L.	ERIRUB	Sedentary	Extend present	Generalist forest	37	140
European pied flycatcher	Ficedula hypoleuca Pallas	FICHYP	Migrant	Irregular	Mature forests	3	4
Common chaffinch	Fringilla coelebs L.	FRICOE	Migrant	Extend present	Generalist forest	40	224
Eurasian jay	Garrulus glandarius L.	GARGLA	Sedentary	Extend present	Generalist forest	52	205
Red crossbill	Loxia curvirostra L.	LOXCUR	Sedentary	Humid areas	Coniferous forests	4	6
Common Nightingale	Luscinia megarhynchos Brehm	LUSMEG	Migrant	Extend present	Humid forests	58	434
Eurasian golden oriole	Oriolus oriolus L.	ORIORI	Migrant	Extend present	Humid forests	52	208
Coal tit	Periparus ater L.	PARATE	Sedentary	Extend present	Coniferous forests	12	17
Eurasian blue tit	Cyanistes caeruleus L.	PARCAE	Sedentary	Extend present	Forests	39	167
European crested tit	Lophophanes cristatus L.	PARCRI	Sedentary	Extend present	Coniferous forests	52	204
Great tit	Parus major L.	PARMAJ	Sedentary	Extend present	Generalist forest	65	438
Western bonelli's warbler	Phylloscopus bonelli Vieillot	PHYBON	Migrant	Extend present	Generalist forest	49	167
Common chiffchaff	Phylloscopus collybita Vieillot	PHYCOL	Sedentary	Humid areas	Humid forests	7	8
Iberian green woodpecker	Picus viridis L.	PICVIR	Sedentary	Extend present	Generalist forest	47	108
Common firecrest	Regulus ignicapilla Temminck	REGIGN	Sedentary	Extend present	Forests	18	46
Eurasian nuthatch	Sitta europaea L.	SITEUR	Sedentary	Humid areas	Mature forests	1	3
Eurasian blackcap	Sylvia atricapilla L.	SYLATR	Sedentary	Extend present	Humid forests	39	153
Garden warbler	Sylvia borin Boddaert	SYLBOR	Migrant	Humid areas	Humid forests	2	3
Eurasian wren	Troglodytes troglodytes L.	TROTRO	Sedentary	Extend present	Forests	45	236
Common blackbird	Turdus merula L.	TURMER	Sedentary	Extend present	Generalist forest	66	541
Song thrush	Turdus philomelos Brehm	TURPHI	Sedentary	Humid areas	Forests	10	14

linked to habitat selection patterns and resource distribution alone but also to behavioural constraints (Prodon, 2021). Consequently, severe habitat changes may promote dispersal and limit site tenacity, above all in the case of forest specialists (McNicholl, 1975). However, generalist species demonstrate a capacity to effectively maintain their territorial behaviour and site fidelity in burnt areas due to their adaptability to changing conditions (Brunet et al., 2011).

Climate change and human activities have contributed to the modification of fire regimes over recent centuries (Brotons et al., 2013). However, numerous questions regarding how the spatial and temporal legacy of fire influences biodiversity are still to be addressed (Driscoll et al., 2010). The landscape mosaics created by wildfires are also little understood and studied. Consequently, the aim of our study was to identify the underlying factors that drive the temporal variations occurring in forest bird populations and communities after wildfires, with a particular focus on the influence of site characteristics, fire behaviour, fire-induced habitat changes and salvage logging. To do so, we conducted 685 transects in 68 burnt areas in Catalonia (NE Iberian Peninsula), ranging from one to 11 years post-fire. We predicted that the presence of forest species in recently burnt areas would be characterized by (1) a higher frequency of forest species occurrence in the first years after the fire compared to the subsequent years due to site fidelity, (2) greater occurrence of forest birds in humid areas than in dry areas, since in humid places favour plant succession and recover will take place earlier (Zavala et al., 2000; Puig-Gironès et al., 2017), and (3) higher occurrence rates and diversity in areas with low fire severity and high heterogeneity of post-fire habitats. As well, (4) the presence of unburnt patches would promote the occurrence and diversity of forest species and (5) salvage logging practices would reduce forest bird occurrence and diversity in recently burnt areas. By exploring these factors using a common framework, we aimed to provide valuable insights into the management and conservation of post-fire bird communities in Mediterranean ecosystems.

2. Material and methods

2.1. Study region

The study was conducted in Catalonia (NE Iberian Peninsula; Fig. 1), a region of around 32,100 km^2 with great environmental heterogeneity due to its sharp climatic and geological gradients. Most of this region enjoys a Mediterranean climate (Piñol et al., 1998) in which the water deficit (when the evaporative demand exceeds available soil moisture) is the main environmental stressor (Stephenson, 1998). Human presence since prehistoric times has resulted in significant changes in the composition and distribution of the dominant plant species. Today, the land cover chiefly consists of forests (31%), evergreen shrublands (29%) and agricultural land (33%) (Vallecillo et al., 2013). Fire is a major landscape driver in this region, with about 25% of wildland area having been burnt since 1975 (Brotons et al., 2013). Furthermore, land abandonment has led to extensive woody plant encroachment and more areas being affected by wildfires in recent years (Duane et al., 2021). Recent fires ensuing during extreme meteorological conditions promoted by global warming have burnt with unprecedented intensity (Pausas and Fernández-Muñoz, 2012).

2.2. Sampling design

We studied 68 burnt areas (up to 11 years after fire) throughout Catalonia ranging in size from 51 to 6,647 ha (Zozaya et al., 2010) and affected by wildfires between 2000 and 2011. Within each fire perimeter, we established 500×200-m transects and surveyed birds once a year over a period of 1–9 years (Fig. 1). Transects were placed at a minimum distance of 150 m from each other and at least 50 m from the edge of the burnt area. However, the majority of transects were >100 m from the perimeter and in those that were closer to the perimeter (i.e. 50–100 m from the edge) only one end of the transect was affected. In the unlikely event of birds being seen or heard outside the burnt area, observers were trained to note these observations accordingly and they were excluded from analyses (<1%). We conducted 3,048 bird censuses over the 685 transects, with the number of transects in each area depending on the size of the burnt area (range: 2–41). Each survey lasted 15 min divided into three five-minute periods and covered about 165 m in length. Birds were counted if heard or seen and were placed in one of three distance bands (0–25, 25–50 or 50–100 m). Surveys were conducted once during the breeding season (from 10 May–15 June) in good weather conditions (i.e. no rain or strong wind) within the first four hours after sunrise by experienced ornithologists walking at about 2 km per hour (Bibby et al., 2000). The criteria for the choice of transects and the sampling protocol are fully explained in Zozaya et al. (2010).

2.3. Bird data

Bird species often specialize in particular habitats and are useful as indicators of habitat structures (Herrando et al., 2016), so studying their temporal occurrence after a wildfire can provide valuable information (Puig-Gironès and Real, 2022). Here, we selected Mediterranean forest bird species (Table 1) previously defined as those that occur in mature, humid or open forests but excluded ecotone, edge or shrubland specialists (Prodon and Lebreton, 1981; Herrando et al., 2016; Franch et al., 2021). Additionally, we also refer as forest specialists those bird species that have a strong preference for forest habitats and are unlikely to be found outside of those habitats. To measure the relative abundance of forest birds, we used the frequency of occurrence (number of presences/number of surveys; range 0–1) per transect. We focused on the frequency of occurrence of species that inhabit Mediterranean habitats and occur in at least 12 of the 68 burnt areas studied, and placed into the 100 m distance bands. Thus, we excluded from individual analyses tree pipit (*Anthus trivialis* L.), European pied flycatcher (*Ficedula hypoleuca* Pallas), red crossbill (*Loxia curvirostra* L.), common chiffchaff (*Phylloscopus collybita* Vieillot), Eurasian nuthatch (*Sitta europaea* L.), garden warbler (*Sylvia borin* Boddaert) and song thrush (*Turdus philomelos* Brehm), seven species that are unlikely to breed in the study area. However, we included the total (27) forest species in our diversity analyses (Table 1).

2.4. Environmental variables

Environmental variables were recorded at two different scales: in burnt areas (time since fire and distance to unburnt patches) and in transects (water deficit, pre-fire forest percentage, fire severity, fire heterogeneity, unburnt patches density, salvage logging occurrence and presence of wood debris piles). However, it is important to note that transects used was at least 100,000 m^2 (i.e., 10 ha). For example, in a burned area of 50 ha, approximately 2 to 3 transects were placed, covering between 40 and 60% of the total burnt area. Therefore, the environmental variables (mainly pre-fire forest percentage, fire severity and fire heterogeneity) will be assimilated to landscape-scale variables (see below for methodological details). 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 six months after the fire, i.e. TSF = 1 means that 7–13 months had elapsed since the fire.

Water deficit (WD), our indicator of aridity (both terms are used hereafter interchangeably), was calculated for each transect (in June–May) using data on 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 based on data from meteorological stations (one station/64 km^2). We used the equation established by Thornthwaite (Thornthwaite, 1948; Black, 2007): WD = PET – ETr that gave values of between −137.9 and 538.3 mm for our transects, although in our analyses we set all negative values to 0 mm. We replaced negative values by zeros to mitigate outliers, given the limited number of transects with values less than 0 (2% of the total).

Using QGIS we drew a 100-m buffer around the transect path (Fig. 1) to extract the percentage cover of pre-fire CORINE forest habitats: Agroforestry areas, Broad-leaved forest, Coniferous forest and Mixed forest. These habitat categories were determined using the CORINE land cover dataset, specifically the maps available before the occurrence of each 68 fires (Büttner et al., 2021). For each burnt area, the CORINE map that was temporally closest to the fire event was used to ensure that the data coincided as closely possible to the pre-fire habitats. To assess the severity and heterogeneity of a wildfire within each 100-m buffer around the transect path, we used the transect buffer and Landsat-based (Loveland and Dwyer, 2012) normalized burn ratio (NBR) approach, which is widely used in fire research (Key and Benson, 2006). Specifically, we calculated the mean of the differenced normalized burn ratio (dNBR) per transect to evaluate severity, and measured the difference between pre-fire NBR values from Landsat images (24.85±33.14 days before fire) and post-fire (20.53±28.50 days after fire) NBR values for vegetation conditions (Veraverbeke et al., 2010). In addition, we used the standard deviation of dNBR to assess the spatial heterogeneity of fire effects within each 100-m buffer around the transect path. This variable allowed us to quantify the variability in fire severity, with high standard deviation values indicating greater variability and low values suggesting more consistent severity (Puig-Gironès et al., 2023a).

To assess the effect of unburnt vegetation patches within burnt areas on forest birds we followed a step-by-step process. First, unburnt areas of >625 m^2 (corresponding to 25×25-m pixels) were selected within the burnt areas. We assumed that such patches would be sufficiently large area to regularly attract forests birds (Watson et al., 2012a). To identify unburnt patches, we used normalised burn ratio (dNBR) values, where individual pixels with dNBR values less than −251 were considered as unburnt patches. Subsequently, for each transect, we established a series of points, spaced 10 m apart, along the entire length of the transect. To calculate distances, we determined the minimum distance from each of these points to the nearest unburnt patch or to the burnt area perimeter, selecting the closest of the two options (Fig. 1). Lastly, for each transect, the mean minimum distance and its standard deviation were calculated.

Finally, to assess the effects of the unburnt patches density, salvage logging and wooden debris piles within the wildfire area, ordinal variables were calculated at both the start and end of each transect. Unburnt patch density values ranged from 0 (completely burnt) to 2 (high presence of unburnt patches) for each sampling station. Similarly, salvage logging values ranged from 0 (completely unlogged) to 2 (completely logged), and the presence of woody debris piles was assessed with values ranging from 0 (absent) to 2 (abundant) at each sampling station. Cumulative values of each variable were obtained by summing the scores of the two sampling stations per transect, resulting in a scale of 0 to 4. Consequently, unburnt or lightly burnt patches, which can serve as habitat islands, were scored from 0 (the entire transect area was completely burnt) to 4 (numerous unburnt patches throughout the transect area). Salvage logging was scored from 0 (no logging activity) to 4 (complete logging of the area). Lastly, the presence of piles of wooden debris was recorded from 0 (absent) to 4 (abundant). It is noteworthy that logging can lead to woody debris piles, however, salvage logging and woody debris presence are not necessarily correlated. Salvage logging covers a wide range of actions, from complete tree removal for chipping to the forming debris piles for erosion control. Woody debris amounts can greatly differ based on the logging approach.

2.5. Data analyses

We used an information-theoretical approach to examine the relationships between the 20 individual forest bird species, the α-diversity and β-diversity (response variables) and predictor variables. Forest bird richness was used as the diversity measure, whereby the α-diversity was the number of species per transect/year, the β-diversity was calculated using a modified Whittaker (1972) equation: $\beta\text{-diversity} = 1/(\gamma\text{-diversity}/\alpha\text{-diversity}) - 1$), where the γ-diversity was the total number of forest bird species recorded in a sampling burnt area/year. The Whittaker index has proven to be the most robust index for measuring replacement between communities (Magurran, 1988). Our modified equation of Whittaker's, directly measuring species compositional differences between sites through a reciprocal transformation, enhances the interpretability and positive scaling of the results. To allow valid comparisons of the adjusted β-diversity values by having a variety of γ-diversity for each site and year, we implemented a standardization procedure. This standardization was performed immediately after calculating the site- and year-specific β-diversity. In particular, we standardized the β-diversity values using the formula: $(\beta\text{-diversity}/\gamma\text{-diversity})*10$. This method approach addresses the variations and different levels of γ-diversity observed across sites and years. By dividing β-diversity by γ-diversity, we obtain a ratio that quantifies the extent to which local diversity (α-diversity) diverges from total regional diversity (γ-diversity). Importantly, this standardization procedure maintains the relative relationships between β-diversity values among sites while fitting them to a consistent scale from 0 to 10. The intention of standardizing β-diversity values is to ensure their comparability. Thus, this adjustment allows for effective comparisons between sites and years using the same numerical scale. All diversity variables were calculated for the entire pool of forest bird species; two subsets of species based on migratory behaviour were analysed, sedentary or migrant (Table 1), by calculating their α-diversity and β-diversity.

We used generalized additive mixed models (GAMMs) to evaluate the role of the variables such as area and fire characteristics related to post-fire habitat suitability on the occurrence of forest bird species. GAMMs are a powerful regression analysis tool that employs smoothed splines fitted to the explanatory variables rather than the original values of the variables (Wood, 2017). First, the time since fire and water deficit were included as smoothed explanatory variables, and the pre-fire forest percentage, fire severity and fire heterogeneity were included as linear term explanatory variables. The mixture of non-linear (smoothed) and linear (unsmoothed) predictors was in the interest of maintaining simplicity of the model results interpretation, as well as reducing the risk of overfitting, based on prior knowledge and exploration of the data (see for example Puig-Gironès et al., 2017; Puig-Gironès et al., 2022). The GAMMs had different error structures due to the origin of the data: the 20-individual forest bird occurrence models had a binomial error structure and log link function; α-diversity (species richness) models used Poisson error structures and log link functions; and the β-diversity models had a Gaussian error structure. For α-diversity models, overdispersion was assessed and no excessive variability beyond Poisson distribution was found. For β-diversity models, despite standardized values, the distribution closely approximated Gaussian distribution, supported by exploratory analysis and data distribution evaluation. We included transects nested within the burnt area as a random factor to control for possible site-based differences. To enable better comparisons between species and reduce differences in detectability, we used the frequency of occurrence (0–1) of species in censuses instead of relative abundance. In order to meet assumptions, the pre-fire forest percentage was arcsin transformed, while fire severity, fire heterogeneity and distances were transformed using base 10 logarithm. Finally, the model-

Table 2

Effect of environmental variables on forest bird species and community. Summary of generalized additive mixed models (GAMMs) showing the variables related to post-fire habitat suitability used to analyse the occurrence and diversity of the forest bird species in 68 burnt areas in Catalonia affected by wildfires between 2000 and 2011. Models include parameter coefficient and standard error (±SE), and only display the coefficient sign (+or –) for non-significant variables. The effective degrees of freedom (edf) are shown for significant smoothed variables (time since fire and water deficit).

Common name	Scientific name	Intercept	Pre-fire forest percentage	Fire severity	Fire heterogeneity	Time since fire	Water deficit
Long-tailed tit	Aegithalos caudatus	(–)	(+)	(–)	(+)	3.58	
Short-toed treecreeper	Certhia brachydactyla	(–)	0.93±0.19	−3.36 ± 0.91	2.47±0.72	2.54	1.00
Common wood pigeon	Columba palumbus	(+)	(+)	−2.36 ± 0.56	1.41±0.43	1.06	1.00
Common cuckoo	Cuculus canorus	−6.43 ± 3.03	(+)	(+)	1.17±0.60	5.67	
Great spotted woodpecker	Dendrocopos major	(–)	(+)	(–)	(+)	1.74	2.07
European robin	Erithacus rubecula	(–)	(+)	−2.53 ± 1.06	3.15±0.84	4.57	1.00
Common chaffinch	Fringilla coelebs	−6.34 ± 3.37	0.99±0.17	(–)	1.28±0.65	4.45	1.00
Eurasian jay	Garrulus glandarius	(–)	0.36±0.15	(–)	(+)	2.21	2.31
Common Nightingale	Luscinia megarhynchos	(+)	(+)	−1.78 ± 0.73	1.45±0.51	6.57	1.00
Eurasian golden oriole	Oriolus oriolus	(+)	0.41±0.18	−1.70 ± 0.74	(+)	1.00	
Coal tit	Periparus ater	(–)	(+)	(+)	(–)		
Eurasian blue tit	Cyanistes caeruleus	(–)	0.58±0.17	(–)	1.85±0.66	1.85	1.00
European crested tit	Lophophanes cristatus	−5.62 ± 2.90	0.42±0.18	(–)	2.69±0.63	3.04	
Great tit	Parus major	(–)	0.47±0.11	(–)	0.87±0.38	5.91	1.00
Western bonelli's warbler	Phylloscopus bonelli	(+)	0.62±0.22	−4.54 ± 0.97	3.84±0.83	2.25	1.00
Iberian green woodpecker	Picus viridis	(–)	(+)	(–)	(+)	2.02	
Common firecrest	Regulus ignicapilla	(–)	(+)	(+)	(+)		1.00
Eurasian blackcap	Sylvia atricapilla	(–)	0.39±0.21	−1.97 ± 0.98	2.22±0.70	4.01	1.00
Eurasian wren	Troglodytes troglodytes	−9.97 ± 4.00	(+)	(+)	2.47±0.82	4.17	2.41
Common blackbird	Turdus merula	(–)	(+)	(–)	0.93±0.37	3.86	1.24
Alpha diversity		(+)	0.20±0.05	−0.85 ± 0.22	0.86±0.16	6.07	2.22
Beta diversity		(+)	(+)	(–)	0.67±0.23	1.59	5.60
Resident species		(+)	0.23±0.051	−0.78 ± 0.23	0.89±0.17	4.84	2.28
Resident beta diversity		(+)	(+)	(–)	0.49±0.17		5.92
Migrant species		(+)	0.13±0.06	−1.19 ± 0.26	0.70±0.19	5.82	1.00
Migrant beta diversity		(+)	(–)	(–)	(+)	1.00	1.00

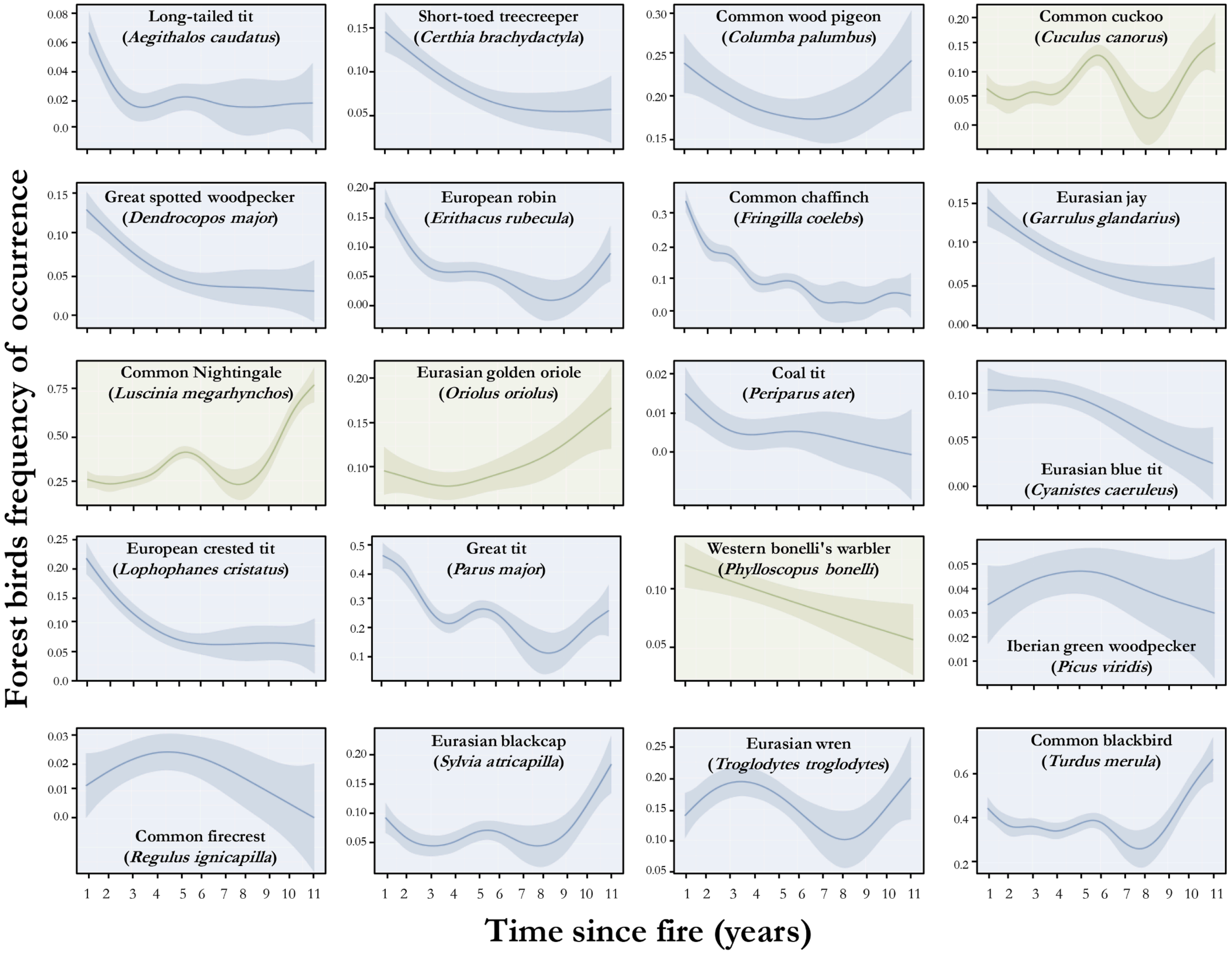

Fig. 2. Marginal effects of forest bird species occurrence over time. The influence of time since fire on forest bird species occurrence. Trend lines and shaded standard errors (95 % confidence intervals) were obtained from GAMM model estimates. Green species correspond to large *trans*-saharian migrants bird on the study area.

predicted post-fire and water deficit responses of birds were classified into categories following Watson et al. (2012).

Secondly, to examine the importance of the spatial characteristics across both burnt and transect scales for the forest bird community, we used generalized linear mixed models (GLMMs). The explanatory variables included the size of the burnt area, the distance to the nearest unburnt area, the standard deviation of the distance to the nearest unburnt area, and the transect-scale density of unburnt patches. Lastly, we used GLMMs to assess the effects of post-fire treatments on the forest bird community, with the occurrence of salvage logging and the presence of piles of wood debris as explanatory variables. For all GLMM analyses, we included the Poisson error structure for α-diversity (species richness) models, while β-diversity models were performed with a Gaussian error structure and log link functions. Moreover, we constructed binomial error structure models for each of the 20-forest species. To account for possible variability, transects nested within the burnt area were considered as a random factor.

Multicollinearity diagnostics and variability assessments (outliers: unusual influential data points; Zuur et al. (2010)) were performed before modelling by quantifying generalized variance-inflation factors (GVIF[1/(2 df)]) for each fixed factor (Fox and Monette, 1992), where GVIF values ≤2.5 (arbitrary threshold) suggested collinearity. Multicollinearity diagnostics were performed for unsmoothed variables; however, no collinearities were found. All analyses were performed with R software (R Development Core Team, 2017) and the *gamm4* (Wood and Scheipl, 2014), *lme4* (Bates et al., 2015), *car* (Fox and Weisberg, 2011) and *MuMIn* (Bartoń, 2016) packages. Finally, the model-predicted post-fire responses of birds were classified into categories following Watson et al. (2012b).

3. Results

3.1. Forest bird occurrence

During the study, a total of 7,471 detections of the selected 27 forest bird species were recorded in the 68 burnt areas, which individually held 2–23 forest species (mean = 13.5 species/burnt area). Individual transects harboured 0–18 forest bird species (mean = 6.2 species/transect). The most common species (occurring in >25 % of locations) were, in descending order, common blackbird (*Turdus merula* L.), great tit (*Parus major* L.), common wood pigeon (*Columba palumbus* L.), common nightingale (*Luscinia megarhynchos* Brehm), Eurasian jay (*Garrulus glandarius* L.), Eurasian golden oriole (*Oriolus oriolus* L.) and European crested tit (*Lophophanes cristatus* L.), of which five are sedentary and two migrant species (Table 1). The six species with the highest frequency of occurrence accounted for 61% of the total detections: common blackbird

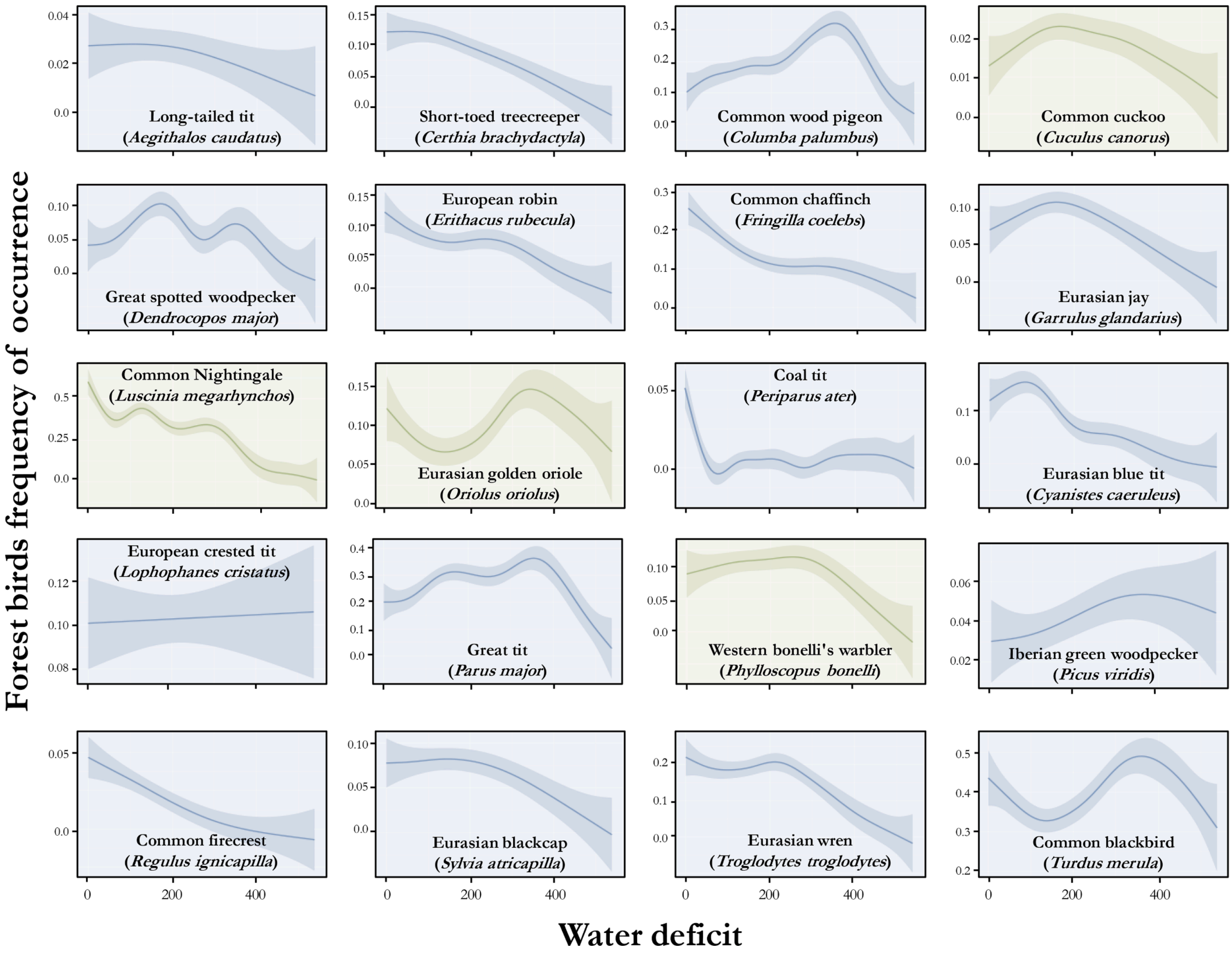

Fig. 3. Marginal effects of forest bird species occurrence over water deficit. The influence of the gradient of water deficit on the distribution of forest bird species occurrence. Trend line and shaded standard error (95 % confidence intervals) were obtained from GAMM model estimates. Green species correspond to large *trans*-saharian migrants bird on the study area.

with 1177 detections, common nightingale with 1031, great tit with 852, common wood pigeon with 604, Eurasian wren (*Troglodytes troglodytes* L.) with 508 and common chaffinch (*Fringilla coelebs* L.) with 401 detections.

3.2. Patterns of forest bird species in response to fires

In the 68 burnt areas analysed, our Generalized Additive Mixed Models (GAMMs) revealed significant associations between environmental variables and the presence of forest bird species (Table 2). Specifically, 18 out of the 20 forest bird species examined showed significant relationships with time since fire, and fourteen were significantly related to the water deficit. The forest bird community exhibited various post-fire responses (Watson et al., 2012b), including primarily irruptive (7 species) and inverse-irruptive (5) trends related to time since fire (Fig. 2), as well as incline (8 species) and bell-shaped (7) were the most frequent trends associated with water deficit (Fig. 3). Therefore, in general, most forest bird species tended to decrease their frequency of occurrence from the first to the sixth year after fire. However, migratory species dis not exhibit substantial changes in the first years, but tended to increase their occurrence from the sixth year onwards. Regarding water deficit, the occurrence of almost all species decreased when the transect was more arid, being this trend relevant from 300 mm onwards. On the other hand, seven out of 20 forest bird species analysed had a negative relationship with fire severity (Table 2). Lastly, thirteen species were significantly positively related to fire heterogeneity (Fig. S1), while nine were positively related to the pre-fire percentage of forest.

Furthermore, spatial characteristics of the burnt areas significantly affected forest bird populations (Table 3). Specifically, five out the 20 forest bird species exhibited negative relationships with burnt area size, while seven were negatively affected by large distances to unburnt patches. Additionally, our Generalized Linear Mixed Models (GLMMs) showed that the unburnt patch density had a significantly positive relationship with 17 species (Fig. 4), while salvage logging was related to 12 species, with nine of them displaying a negative association (Fig. S2). Lastly, the presence of piles of wood debris was related with nine forest bird species, six of which exhibited a positive relationship (Table 4).

3.3. Forest bird diversity responses to wildfires

Diversity models showed similar relationships to those found for the individual species (Table 2). All diversity parameters for forest birds, sedentary forest birds and migrant forest birds – with the exception of the β-diversity of resident species – decreased with time since fire but then increased again after about seven years post-fire in an inverted-bell trend (Fig. 5). Similarly, all forest bird diversity variables decreased with

Table 3

Effect of spatial characteristics of the burnt areas on forest bird species and community. Summary of generalized linear mixed models (GLMMs) used to analyse the occurrence and diversity of the forest bird species in 68 burnt areas in Catalonia affected by wildfires between 2000 and 2011. Models include parameter coefficient and standard error (±SE), and only display the coefficient sign (+or –) for non-significant variables.

Common name	Scientific name	Intercept	Distance to unburn patches	Distance standard deviation	Burt area size	Unburnt patches density
Long-tailed tit	Aegithalos caudatus	(–)	(–)	(–)	(–)	0.68±0.10
Short-toed treecreeper	Certhia brachydactyla	(–)	(–)	(+)	−1.05 ± 0.47	0.55±0.07
Common wood pigeon	Columba palumbus	(+)	−0.79 ± 0.20	(+)	−0.62 ± 0.29	0.27±0.05
Common cuckoo	Cuculus canorus	(–)	(–)	(–)	(–)	(+)
Great spotted woodpecker	Dendrocopos major	(–)	(–)	(+)	(–)	0.26±0.08
European robin	Erithacus rubecula	(–)	(–)	(+)	(–)	0.63±0.09
Common chaffinch	Fringilla coelebs	(–)	(–)	(–)	(+)	0.25±0.07
Eurasian jay	Garrulus glandarius	(+)	(–)	(–)	−0.86 ± 0.31	0.12±0.06
Common Nightingale	Luscinia megarhynchos	(–)	−0.48 ± 0.21	(+)	(+)	0.24±0.05
Eurasian golden oriole	Oriolus oriolus	(–)	−0.61 ± 0.27	(+)	(–)	0.14±0.07
Coal tit	Periparus ater	(–)	(–)	(–)	(–)	(+)
Eurasian blue tit	Cyanistes caeruleus	−3.90 ± 1.59	(–)	(+)	(+)	0.30±0.08
European crested tit	Lophophanes cristatus	(+)	−0.58 ± 0.29	(+)	−1.11 ± 0.38	0.45±0.07
Great tit	Parus major	(–)	(–)	(–)	(–)	0.28±0.05
Western bonelli's warbler	Phylloscopus bonelli	(+)	−1.14 ± 0.34	−0.93 ± 0.48	(–)	0.62±0.08
Iberian green woodpecker	Picus viridis	(+)	(–)	(+)	−1.06 ± 0.33	(+)
Common firecrest	Regulus ignicapilla	−4.53 ± 2.34	−1.23 ± 0.67	(+)	(–)	0.50±0.15
Eurasian blackcap	Sylvia atricapilla	−2.90 ± 1.51	−0.98 ± 0.32	(+)	(+)	0.41±0.08
Eurasian wren	Troglodytes troglodytes	−4.71 ± 1.85	(+)	(+)	(–)	0.50±0.08
Common blackbird	Turdus merula	(+)	(–)	(–)	(–)	0.27±0.04
Alpha diversity		1.94±0.43	−0.29 ± 0.07	(–)	(–)	0.15±0.01
Beta diversity		6.56±0.73	(–)	(–)	−1.92 ± 0.28	0.18±0.03
Resident species		1.77±0.44	−0.25 ± 0.08	(–)	−0.35 ± 0.17	0.17±0.01
Resident beta diversity		4.40±0.62	(–)	(–)	−1.28 ± 0.24	0.12±0.02
Migrant species		(–)	−0.31 ± 0.09	(+)	(–)	0.17±0.02
Migrant beta diversity		0.54±0.15	(–)	(+)	−0.16 ± 0.06	0.01±0.006

greater water deficit, with the exception of the β-diversity that increased in drier regions, where the gamma diversity is lower and high values of β-diversity can be easily attained. Fire severity negatively affected α-diversity and migrant species, while the pre-fire percentage of forest positively influenced α-diversity and resident species. Complementarily, fire heterogeneity showed positive relationships with all forest diversity parameters, being non-significant only for migrant β-diversity (Table 2).

Regarding spatial effects, the distance to unburnt areas negatively affected α-diversity and resident and migrant species (Table 3). On the other hand, the size of the burnt areas was negatively related to forest bird species diversity. Moreover, more unburnt patches were positive for all diversity parameters (Fig. 5).

Lastly, our data analyses showed moderate effects for post-fire management on forest bird diversity (Table 4). Salvage logging showed a significant and negative effect on α-diversity and resident species richness (Fig. 5). It is important to note that these results relate to diversity regardless of species identity as most individual species are clearly negatively affected by logging (Fig. S2). On the other hand, the more piles of wood debris there were, the greater the resident species richness but lower the migrant species richness (Fig. 5). Although the three β-diversity variables (all forest birds, residents and migrants) did not show any significant relationship with salvage logging and piles of wood debris, the overriding trend seems to indicate negative effects on β-diversity (Table 4).

4. Discussion

Overall, our results show that the heterogeneity in resource redistribution occurring within burnt habitats rather than fire *per se* are the main drivers behind the observed patterns of forest bird redistribution post-fire (Fahrig et al., 2011). Time since fire is an important factor to explain the occurrence rate of individual forest bird species and their overall diversity in recently burnt Mediterranean areas. Moreover, water deficit, fire heterogeneity, the density of unburnt patches and salvage logging all played a critical role in shaping the overall patterns of forest bird redistribution, which thus underscores their importance in the post-fire occurrence of forest bird populations and diversity.

4.1. *Temporal occurrence of forest species: Site fidelity and aridity effects*

Site fidelity can influence the decision of forest birds to stay or leave after a fire (Prodon and Lebreton, 1981; Pons et al., 2003). Among other factors, birds with high site fidelity – i.e. those more familiar with the area – are more likely to stay and search for necessary resources, while those with low tenacity are more likely to leave and seek suitable habitats elsewhere (Schlossberg, 2009; Piper, 2011). Our results show faster recovery in three of the four migrant forest birds (Common cuckoo, Nightingale, Eurasian golden oriole). Additionally, certain forest specialist species, such as the long-tailed tit, crested tit, and great spotted woodpecker, were underrepresented in our dataset. Some forest specialists may not thrive in relatively young forests (Brunet et al., 2011; Naaf and Kolk, 2015), which are the most frequent in our study area before fires, potentially resulting in their absence immediately after the fire event.

Birds that occupy ephemeral habitats may have lower site fidelity than birds found in more stable habitats like forests (Jones et al., 2007). Thus, site fidelity initially contributes to a higher post-fire presence of forest species (Prodon and Lebreton, 1981; Pons et al., 2003). However, our results indicate a clear reduction in forest bird occurrence 1–6 years after fires, which could be due to the depletion of resources and loss of suitable habitat structure (Franklin et al., 2022). This reduction may also be linked to the fact that adults are frequently faithful to breeding sites, while yearlings tend to disperse away from their natal sites (Schlossberg, 2009). Nine years after the fire, certain recovery is observed, especially among a small number of species, both generalist and migratory. This period is significantly longer than the lifespan of most small passerines (Klimkiewicz et al., 1983) suggesting that the observed recovery involves the influx of new individuals, as well as some input from the survivors' offspring, rather than relying solely on the survival of resident birds. Our model results, which indicate an increase in both species richness and β-diversity, i.e., fostering shifts in species diversity among sites, support this inference over the nine years following the fire. Thus, immediate site fidelity may promote the recovery of forest bird populations if a significant number of forest birds exhibit site fidelity, which means that they are more likely to remain in burnt areas than abandon

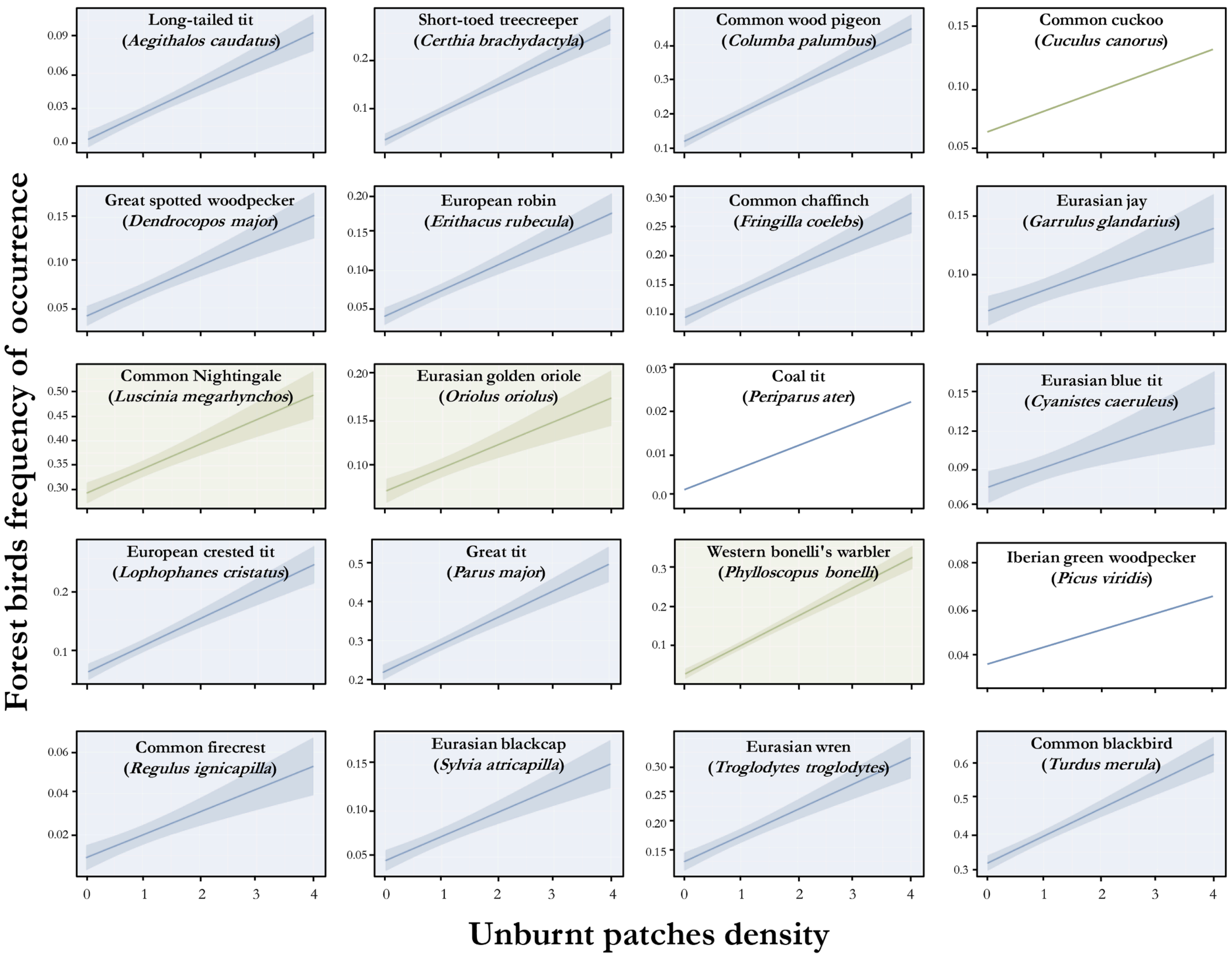

Fig. 4. Marginal effects of forest bird species occurrence over unburnt patches density. The influence of the unburnt patches density on the distribution of forest bird species occurrence. Trend line and shaded standard error (95 % confidence intervals) were obtained from GLMM model estimates. Lines without shaded areas indicate non-significant relationships. Green species correspond to large *trans*-saharian migrants bird on the study area.

them in search of unburnt habitat. This may reduce the immediate fire impact on forest bird communities and facilitate the recolonization of burnt areas by certain bird species. However, this may confound managers' perceptions if they only observe the biodiversity in the first few years after fires. Tenacity increases the diversity of birds in recently burnt area because forest specialist are added to open-habitat colonizers (Prodon and Lebreton, 1981). Nevertheless, this effect has a limited duration, between one and six years after the fire, as shown by our results for species richness and β-diversity, which tends to decrease between one and six years after fire. Thus, understanding the role of site fidelity in the post-fire recovery of bird populations is important for developing effective management and conservation strategies that will promote the resilience of forest bird communities to disturbances.

Establishing cause and effect is challenging due to the limitations of our data. The absence of pre-fire data makes it difficult to differentiate between site fidelity or immigration, an interesting debate about starting points for recovery after wildfire (see for example (Santos et al., 2009; Hale et al., 2022; Puig-Gironès and Pons, 2023). However, focusing on forest birds between 1 and 11 years post-fire offers a unique opportunity to explore this issue. Our results showed an initial decline in the occurrence of many forest birds, forest species richness and β-diversity. Meanwhile, the frequency of open-habitat birds increased in the same 68 burnt areas from surrounding areas (Puig-Gironès et al., 2022). Therefore, if immigrant forest birds drove recovery, populations would be expected to remain stable or grow from the first year, indicating that site fidelity plays an important role in the temporal trends of most studied forest bird species, as other authors have found (Pons et al., 2003; Prodon, 2021). Along these lines, it is important to emphasise that, although site tenacity may play a significant role, it is just the behavioural reason. For birds to remain in an area after fire, thereby ensuring survival and reproduction, a consistent availability of resources (food and shelter) and manageable risks of mortality (e.g. predation) are essential. Therefore, besides site tenacity, what the habitat can offer and the post-fire biota are equally important factors. Consequently, post-fire bird trends are influenced by both behavioural and ecological elements, as suggested by our results for the environmental variables. For example, salvage logging has a negative impact on both overall forest bird diversity and individual species. This underscores the importance of standing trees– even burnt ones – for the persistence of tree-dependent species.

Forest birds were more frequent along humid than dry transects, which has important implications in the context of climate change and increasing fires. Understanding the relationship between water availability and forest bird distribution is crucial for conservation efforts as fires are becoming more frequent and extensive in many regions (Hagger et al., 2019; Roberts et al., 2021). However, our study shows that even

Table 4

Effect of post-fire treatments on open-habitat bird community. Summary of generalized linear mixed models (GLMMs) used to analyse the forest bird diversity in 68 burnt areas in Catalonia affected by wildfires between 2000 and 2011. Models include parameter coefficient and standard error (±SE), and only display the coefficient sign (+or –) for non-significant variables.

Common name	Scientific name	Intercept	Salvage logging	Piles of wood debris
Long-tailed tit	Aegithalos caudatus	−7.86 ± 0.59	−0.48 ± 0.18	(–)
Short-toed treecreeper	Certhia brachydactyla	−3.17 ± 0.33	−0.39 ± 0.07	0.26±0.10
Common wood pigeon	Columba palumbus	−1.40 ± 0.18	(–)	(–)
Common cuckoo	Cuculus canorus	−2.86 ± 0.23	(+)	−0.24 ± 0.11
Great spotted woodpecker	Dendrocopos major	−3.34 ± 0.33	−0.24 ± 0.07	(+)
European robin	Erithacus rubecula	−3.90 ± 0.40	−0.33 ± 0.08	(+)
Common chaffinch	Fringilla coelebs	−3.11 ± 0.41	−0.50 ± 0.07	0.25±0.09
Eurasian jay	Garrulus glandarius	−2.47 ± 0.18	(+)	0.24±0.07
Common Nightingale	Luscinia megarhynchos	−1.18 ± 0.22	0.12 ± 0.04	−0.24 ± 0.07
Eurasian golden oriole	Oriolus oriolus	−2.73 ± 0.19	(–)	(+)
Coal tit	Periparus ater	−12.08 ± 0.003	−0.06 ± 0.002	−1.99 ± 0.003
Eurasian blue tit	Cyanistes caeruleus	−3.40 ± 0.33	−0.29 ± 0.07	0.18±0.09
European crested tit	Lophophanes cristatus	−2.52 ± 0.24	−0.32 ± 0.07	(+)
Great tit	Parus major	−0.93 ± 0.14	−0.16 ± 0.04	(+)
Western bonelli's warbler	Phylloscopus bonelli	−3.30 ± 0.30	−0.23 ± 0.08	(–)
Iberian green woodpecker	Picus viridis	−3.41 ± 0.25	(–)	(–)
Common firecrest	Regulus ignicapilla	−9.38 ± 0.002	0.10 ±0.002	0.01 ±0.001
Eurasian blackcap	Sylvia atricapilla	−3.58 ± 0.30	(+)	0.22±0.09
Eurasian wren	Troglodytes troglodytes	−3.38 ± 0.39	(+)	(+)
Common blackbird	Turdus merula	−0.34 ± 0.14	(–)	(+)
Alpha diversity		0.84±0.09	−0.07 ± 0.01	(+)
Beta diversity		1.59±0.19	(–)	(–)
Resident species		0.57±0.10	−0.11 ± 0.01	0.06±0.02
Resident beta diversity		1.04±0.15	(–)	(+)
Migrant species		−0.66 ± 0.11	(+)	−0.07 ± 0.03
Migrant beta diversity		0.18±0.03	(–)	(–)

humid areas can still experience declines in forest bird diversity and occurrence following a fire, which suggests that water availability is not the only factor at play in post-fire recovery. The slow recovery of vegetation after fires, associated with droughts, can further exacerbate the problem by reducing suitable habitat for these species (Arnan et al., 2007; Puig-Gironès et al., 2017). The ever-increasing frequency and extent of fires is a further challenge to forest bird populations in drier regions.

4.2. The effects of spatial characteristics of the burnt landscape on forest bird occurrence

Our findings show that low fire severity and high heterogeneity facilitate the presence of forest birds and thus suggest that a mosaic of burnt and unburnt areas could be beneficial for maintaining bird populations and diversity, as occurs in the case of Australian mammals (Chia et al., 2016) and American squirrels (Doumas and Koprowski, 2012). The presence and persistence of forest birds in burnt areas are greatly influenced by the spatial characteristics of the burnt landscape, which includes factors such as the shorter distance to suitable unburnt patches and the density of unburnt patches in burnt areas as biological legacies (Watson et al., 2012a). Unburnt patches play a critical role in maintaining biodiversity in fire-prone ecosystems by serving as refuges for species affected by fire or post-fire conditions and by providing important resources for post-fire recovery and recolonization. They also offer habitat heterogeneity, which can enhance ecosystem resilience to future disturbances. Our study highlights that the spatial variation in fire severity associated with wildfires (ranging from unburnt to severely burnt stands) makes an important contribution to the post-fire occurrence of species. The attraction of birds to nearby unburned areas, the density of unburned patches and the heterogeneity of fire severity strongly indicate that post-fire distribution of forest birds is primarily shaped by modifications in critical resources required by these species. This finding supports the idea that resource redistribution, rather than spatial patterns, is the primary driver of forest bird distributions in burnt areas (Fahrig et al., 2011). This pivotal finding highlights the need for further comprehensive research to unravel the underlying factors influencing post-fire diversity and the necessity for strategic management approaches to conserve biodiversity in fire-prone ecosystems.

4.3. Detrimental effects of conventional salvage logging

Salvage logging is a common practice after forest fires (Thorn et al., 2018) but it can have detrimental effects on forest birds. Our results suggest that traditional salvage logging has a negative impact on 10 of the 20 forest bird species analysed, above all on resident species, and forest bird diversity. Although salvage logging can provide economic benefits, it can also lead to a fall in the biological legacies that are crucial for maintaining biodiversity in post-fire landscapes (Elmqvist et al., 2002; DellaSala et al., 2006). Salvage logging can also transform the habitat of the burnt area by removing perches or reducing vegetation cover. For example, woodpeckers can be affected by salvage logging due to the reduction in the amount of available dead wood, snags and living trees (Rost et al., 2013). The non-significant effects of salvage logging on eight species need explanations. Some species may possess ecological traits that make them less vulnerable to salvage logging such as adaptive behaviours, flexible feeding, or broad habitat preferences. Furthermore, these species less dependent on specific microhabitats or resources underscore the importance of trait-based responses and reveal ecological complexities in salvage logging outcomes. Our analyses also indicate that the presence of piles of wood debris is related to an increase in resident species richness, suggesting that the negative effects of salvage logging may be mitigated to some extent by leaving piles of wood debris, which can provide important habitat for certain species (Rost et al., 2010; Puig-Gironès et al., 2020). However, more research is needed to identify effective strategies for managing post-fire landscapes that can balance out ecological and economic considerations and explore alternative approaches prioritizing ecosystem recovery and resilience.

4.4. Management implications and remarks

The findings of this study have substantial implications for the management and conservation of forest bird species in post-fire environments. Identified key factors behind early, post fire bird dynamics include water deficit, fire heterogeneity, the density and proximity of unburnt patches, i.e. resource redistribution and preservation. As a result, several management strategies can be derived from the evidence gathered in our study.

One potential management strategy to promote the occurrence and diversity of forest species is preserve unburnt patches and maintain a

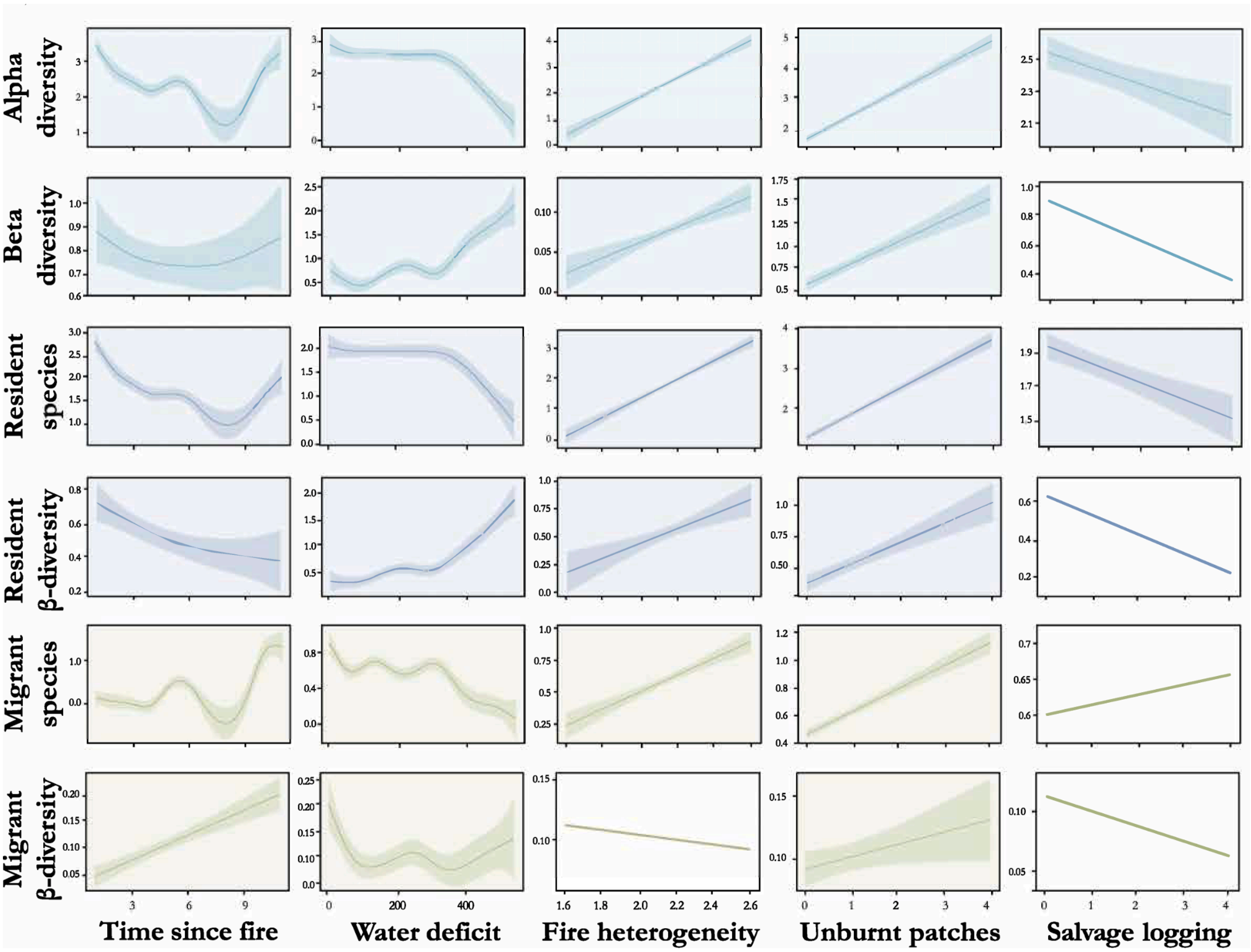

Fig. 5. Marginal effects of forest bird species diversity. Marginal effects (measuring instantaneous rate of change) of the model predictors on forest bird species diversity according to each fixed factor analysed. Trend line and shaded standard error (95 % confidence intervals) were obtained from GAMM and GLMM model estimates. Lines without shaded areas indicate non-significant relationships.

variety of vegetation structures within recently burnt areas. This can provide important refuges (Watson et al., 2012a) for forest species and help to maintain biodiversity in post-fire landscapes. Traditional post-fire salvage logging can negatively affect populations and diversity by altering habitat structure. Therefore, exploring alternative logging practices that minimize these impacts and promote the recovery of forest populations is essential (Pons et al. 2020). Thus, reducing post-fire logging disturbance and promoting the natural regeneration of vegetation can be highly effective. This includes minimizing salvage logging and carefully planning logging operations within the burnt area. Additionally, maintaining unburnt patches within burnt areas can create a mosaic of varying burn severities and vegetation types, enhancing habitat heterogeneity, landscape-scale connectivity and benefiting a diverse range of bird species with different habitat preferences. If salvage logging is conducted, the logging and transit of heavy machinery should be avoided in unburnt areas and across streams, and wood debris should be piled up to encourage vegetation recovery and act as shelter for fauna (Mauri and Pons, 2019).

Another relevant consideration is the impact of climate change on forest bird populations. As the timing and availability of resources such as water and food are altered, it is important to monitor bird populations to ensure their long-term survival. This may involve promoting landscape habitat heterogeneity and reducing the impact of fire on populations. Consequently, in the face of increasing fire severity and frequency, managers may strive for mosaic maintenance since mature forests and open areas are known to relate to lower fire severity. These mosaic will also contribute to the promotion of a variety of forest canopy and understory types that will encourage diverse bird populations (and those of other biota) (Puig-Gironès et al., 2022; Puig-Gironès et al., 2023b). However, as fires intensify and become more frequent, the effectiveness of maintaining a mosaic of forest types may decrease. Although the mosaic may not be able to stop some fires driven by extreme conditions, in most cases this spatial mosaic design will hinder the fire's propagation and, more importantly, facilitate suppression strategies. Continuous monitoring of the effectiveness of these management strategies is critical for understanding their impact on forest bird populations and overall biodiversity, and management approaches must be adapted over time to achieve conservation goals effectively (Puig-Gironès and Real, 2022).

In addition to these management recommendations, it is essential to acknowledge that wildfires are a natural part of ecosystems in both Mediterranean and worldwide contexts (Pausas and Verdu, 2005). Fire determines habitat structure, food availability and spatial mosaics with different regeneration stages, ultimately contributing to greater ecological diversity. However, severe and large fire events associated to emerging fire regimes can lead to sudden changes in communities (Rodrigo et al., 2004), or large scale soil loss (de Luis et al., 2005). Rising water deficit due to temperature increases (Piñol et al., 1998) further affects both vegetation and fauna after wildfires (Arnan et al., 2007; Puig-Gironès et al., 2017; Puig-Gironès et al., 2022). Therefore, effective post-fire management and conservation strategies must consider the complex interplay of factors, including fire suppression, climate change, and salvage logging practices.

To address these interconnected issues, a multifaceted approach taking into account the impacts of fire, climate change, and human interventions is needed. Understanding how environmental gradients affect post-fire processes, especially in susceptible areas near the extreme of these gradients is crucial. This knowledge can improve the management of burnt forests and guide interventions based on the specific environmental and climatic preferences of target species.

CRediT authorship contribution statement

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

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgements

We thank Dani Villero, Elena L. Zozaya and Vicent Vidal for the administration of the bird database, and specially all the field ornihologists who contributed to the DINDIS database. We acknowledge Michael Lockwood for the remarkable improvements in document readability, and Jesús Scrofa for his helpful comments. This study was partially funded by MCIN (Ministerio de Ciencia e Innovación) and AEI (Agencia Estatal de Investigación) through the projects GREENRISK (PID2020-119933RB-C22) and CEX-2018-000828-S “Centro de Excelencia Severo Ochoa” and by Horizon 2020 through Treeads project, grant number 101036926. The database creation and its management was funded by projects CGL2008-05506-CO2/BOS, CGL2005-2000031/BOS and CGL2014-54094-R, granted by the Spanish Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121439.

References

Arnan, X., Rodrigo, A., Retana, J., 2007. Post-fire regeneration of Mediterranean plant communities at a regional scale is dependent on vegetation type and dryness. Journal of Vegetation Science 18, 111–122. https://doi.org/10.1111/j.1654-1103.2007.tb02521.x.

Bartoń K., 2016. Multi-model inference (MuMIn). R package version 1.15.6. In, R package version, Vienna, Austria.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Beale, C.M., Courtney Mustaphi, C.J., Morrison, T.A., Archibald, S., Anderson, T.M., Dobson, A.P., Donaldson, J.E., Hempson, G.P., Probert, J., Parr, C.L., Mayfield, M., 2018. Pyrodiversity interacts with rainfall to increase bird and mammal richness in African savannas. Ecology Letters 21 (4), 557–567.

Bibby, C.J., Burgess, N., Hill, D., Mustoe, S., 2000. Bird Census Techniques. Academic Press, London, UK.

Black, P.E., 2007. Revisiting the Thornthwaite and Mather Water Balance. Journal of the American Water Resources Association 43, 1604–1605. https://doi.org/10.1111/j.1752-1688.2007.00132.x.

Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D’Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J. E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R., Pyne, S.J., 2009. Fire in the Earth system. Science 324, 481–484. https://doi.org/10.1126/science.1163886.

Brotons, L., Herrando, S., Pons, P., 2008. Wildfires and the expansion of threatened farmland birds: the ortolan bunting *Emberiza hortulana* in Mediterranean landscapes. Journal of Applied Ecology 45, 1059–1066. https://doi.org/10.1111/j.1365-2664.2008.01467.x.

Brotons, L., Aquilué, N., de Cáceres, M., Fortin, M.-J., Fall, A., Bohrer, G., 2013. How fire history, fire suppression practices and climate change affect wildfire regimes in Mediterranean landscapes. PLoS One1 8 (5). https://doi.org/10.1371/journal.pone.0062392.

Brunet, J., Valtinat, K., Mayr, M.L., Felton, A., Lindbladh, M., Bruun, H.H., 2011. Understory succession in post-agricultural oak forests: Habitat fragmentation affects forest specialists and generalists differently. Forest Ecology and Management 262, 1863–1871. https://doi.org/10.1016/j.foreco.2011.08.007.

Burrascano, S., Chytrý, M., Kuemmerle, T., Giarrizzo, E., Luyssaert, S., Sabatini, F.M., Blasi, C., 2016. Current European policies are unlikely to jointly foster carbon sequestration and protect biodiversity. Biological Conservation 201, 370–376. https://doi.org/10.1016/j.biocon.2016.08.005.

Büttner G., Kosztra B., Maucha G., Pataki R., Kleeschulte S., Hazeu G., Littkopf A. 2021. CORINE Land Cover Product User Manual (Version 1.0). In, Copernicus Land Monitoring Service. Erişim adresi (19.12. 2021): https://land.copernicus.eu/user-corner/technical-library/clc-product-user-manual.

Cahall, R.E., Hayes, J.P., 2009. Influences of postfire salvage logging on forest birds in the Eastern Cascades, Oregon, USA. Forest Ecology and Management 257, 1119–1128. https://doi.org/10.1016/j.foreco.2008.11.019.

Chia, E.K., Bassett, M., Leonard, S.W., Holland, G.J., Ritchie, E.G., Clarke, M.F., Bennett, A.F., 2016. Effects of the fire regime on mammal occurrence after wildfire: Site effects vs landscape context in fire-prone forests. Forest Ecology and Management 363, 130–139. https://doi.org/10.1016/j.foreco.2015.12.008.

Cochrane, M.A., Barber, C.P., 2009. Climate change, human land use and future fires in the Amazon. Global Change Biology 15, 601–612. https://doi.org/10.1111/j.1365-2486.2008.01786.x.

de Luis, M., Raventos, J., Gonzalez-Hidalgo, J.C., 2005. Fire and torrential rainfall: effects on seedling establishment in Mediterranean gorse shrublands. International Journal of Wildland Fire 14, 413–422. https://doi.org/10.1071/wf05037.

DellaSala, D.A., Karr, J.R., Schoennagel, T., Perry, D., Noss, R.F., Lindenmayer, D., Beschta, R., Hutto, R.L., Swanson, M.E., Evans, J., 2006. Post-fire logging debate ignores many issues. Science 314, 51–52. https://doi.org/10.1126/science.314.5796.51b.

Doumas, S.L., Koprowski, J.L., 2012. Effect of heterogeneity in burn severity on Mexican fox squirrels following the return of fire. International Journal of Wildland Fire 22, 405–413. https://doi.org/10.1071/WF12046.

Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith, D.A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J.E.M., Williams, R.J., York, A., 2010. Fire management for biodiversity conservation: key research questions and our capacity to answer them. Biological Conservation 143 (9), 1928–1939.

Duane, A., Castellnou, M., Brotons, L., 2021. Towards a comprehensive look at global drivers of novel extreme wildfire events. Climatic Change 165, 1–21. https://doi.org/10.1007/s10584-021-03066-4.

Elmqvist, T., Wall, M., Berggren, A.-L., Blix, L., Fritioff, Å., Rinman, U., 2002. Tropical forest reorganization after cyclone and fire disturbance in Samoa: remnant trees as biological legacies. Conservation Ecology 5.

Emlen, J.T., 1970. Habitat selection by birds following a forest fire. Ecology 51, 343–345. https://doi.org/10.2307/1933677.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology letters 14, 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x.

Falcucci, A., Maiorano, L., Boitani, L., 2007. Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. Landscape ecology 22, 617–631. https://doi.org/10.1007/s10980-006-9056-4.

Fox, J., Monette, G., 1992. Generalized collinearity diagnostics. Journal of the American Statistical Association 87, 178–183. https://doi.org/10.1080/01621459.1992.10475190.

Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression. SAGE Publications Inc, Thousand Oaks, CA, USA.

Franch, M., Herrando, S., Anton, M., Villero, D., Brotons, L., 2021. Atles dels ocells nidificants de Catalunya: distribució i abundància 2015–2018 i canvi des de 1980. Institut Català d’Ornitologia & Corssetània Edicions, Barcelona.

Francos, M., Úbeda, X., Tort, J., Panareda, J.M., Cerdà, A., 2016. The role of forest fire severity on vegetation recovery after 18 years. Implications for forest management of Quercus suber L. in Iberian Peninsula. Global and Planetary Change 145, 11–16. https://doi.org/10.1016/j.gloplacha.2016.07.016.

Franklin, M.J., Major, R.E., Bedward, M., Price, O.F., Bradstock, R.A., 2022. Forest avifauna exhibit enduring responses to historical high-severity wildfires. Biological Conservation 269, 109545. https://doi.org/10.1016/j.biocon.2022.109545.

Georgiev, K.B., Chao, A., Castro, J., Chen, Y.-H., Choi, C.-Y., Fontaine, J.B., Hutto, R.L., Lee, E.-J., Müller, J., Rost, J., Żmihorski, M., Thorn, S., Barlow, J., 2020. Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities. Journal of Applied Ecology 57 (6), 1103–1112.

Greenwood, P.J., 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28, 1140–1162. https://doi.org/10.1016/S0003-3472(80)80103-5.

Hagger, V., Wilson, K., England, J.R., Dwyer, J.M., 2019. Water availability drives aboveground biomass and bird richness in forest restoration plantings to achieve carbon and biodiversity cobenefits. Ecology and Evolution 9, 14379–14393. https://doi.org/10.1002/ece3.5874.

Hale, S., Mendoza, L., Yeatman, T., Cooke, R., Doherty, T., Nimmo, D., White, J.G., Andersen, A., 2022. Evidence that post-fire recovery of small mammals occurs primarily via in situ survival. Diversity and Distributions 28 (3), 404–416.

Herrando, S., Brotons, L., Anton, M., Páramo, F., Villero, D., Titeux, N., Quesada, J., Stefanescu, C., 2016. Assessing impacts of land abandonment on Mediterranean biodiversity using indicators based on bird and butterfly monitoring data. Environmental Conservation 43, 69–78. https://doi.org/10.1017/S0376892915000260.

Jones, S.L., Dieni, J.S., Green, M.T., Gouse, P.J., 2007. Annual return rates of breeding grassland songbirds. The Wilson Journal of Ornithology 119, 89–94. https://doi.org/10.1676/05-158.1.

Keeley, J.E., 1986. Resilience of Mediterranean shrub communities to fires. In: Dell, B., Hopkins, A.J.M., Lamont, B.B. (Eds.), Resilience in Mediterranean-type Ecosystems. Dr W. Junk Publishers, Dordrecht, The Netherlands, pp. 95–112.

Kelly, L.T., Brotons, L., 2017. Using fire to promote biodiversity. Science 355, 1264–1265. https://doi.org/10.1126/science.aam7672.

Key C.H., Benson N.C., 2006. Landscape assessment (LA). In: Lutes, D.C., Keane, R.E., Caratti, J.F., Key, C.H., Benson, N.C., Sutherland, S., Gangi, L.J. (Eds.), FIREMON: Fire effects monitoring and inventory system. Gen. Tech. Rep. RMRS-GTR-164-CD. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 1-55.

Klimkiewicz, M.K., Clapp, R.B., Futcher, A.G., 1983. Longevity records of North American birds: remizidae through parulinae. Journal of Field Ornithology 54, 287–294.

Kutiel, P., Kutiel, H., Lavee, H., 2000. Vegetation response to possible scenarios of rainfall variations along a Mediterranean–extreme arid climatic transect. Journal of Arid Environments 44, 277–290. https://doi.org/10.1006/jare.1999.0602.

Lindenmayer, D.B., Noss, R.F., 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology 20, 949–958. https://doi.org/10.1111/j.1523-1739.2006.00497.x.

Lopez, G., Moro, M.J., 1997. Birds of Aleppo pine plantations in south-east Spain in relation to vegetation composition and structure. Journal of Applied Ecology 34, 1257–1272. https://doi.org/10.2307/2405236.

Loveland, T.R., Dwyer, J.L., 2012. Landsat: Building a strong future. Remote Sensing of Environment 122, 22–29. https://doi.org/10.1016/j.rse.2011.09.022.

Magurran, A.E., 1988. Ecological diversity and its measurement. Princeton University Press, New Jersey, US.

Mauri, E., Pons, P., 2019. Handbook of good practices in post-wildfire management. Universitat de Girona, Girona.

McNicholl, M.K., 1975. Larid site tenacity and group adherence in relation to habitat. The Auk 92, 98–104. https://doi.org/10.2307/4084420.

Moreira, F., Russo, D., 2007. Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. Landscape Ecology 22, 1461–1476. https://doi.org/10.1007/s10980-007-9125-3.

Naaf, T., Kolk, J., 2015. Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation. Biological Conservation 182, 155–163. https://doi.org/10.1016/j.biocon.2014.12.002.

Nice, M.M., 1941. The role of territory in bird life. American midland naturalist 26 (3), 441.

Ninyerola M., Pons X., Roure J.M., Martín V.J., Raso J.M., Clavero P., 2003. Atles Climàtics de Catalunya. CD-ROM. Servei Meteorològic de Catalunya y Departament de Medi Ambient de la Generalitat de Catalunya, Barcelona. ISBN: 84-932860-5-2.

Pausas, J.G., Bradstock, R.A., Keith, D.A., Keeley, J.E., Fire Network, G.C.T.E., 2004. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85, 1085–1100. https://doi.org/10.1890/02-4094.

Pausas, J.G., Fernández-Muñoz, S., 2012. Fire regime changes in the Western Mediterranean Basin: from fuel-limited to drought-driven fire regime. Climatic change 110, 215–226. https://doi.org/10.1007/s10584-011-0060-6.

Pausas, J.G., Parr, C.L., 2018. Towards an understanding of the evolutionary role of fire in animals. Evolutionary Ecology 32, 113–125. https://doi.org/10.1007/s10682-018-9927-6.

Pausas, J.G., Verdu, M., 2005. Plant persistence traits in fire-prone ecosystems of the Mediterranean basin: a phylogenetic approach. Oikos 109, 196–202. https://doi.org/10.1111/j.0030-1299.2005.13596.x.

Piñol, J., Terradas, J., Lloret, F., 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. Climatic Change 38, 345–357. https://doi.org/10.1023/a:1005316632105.

Piper, W.H., 2011. Making habitat selection more “familiar”: a review. Behavioral Ecology and Sociobiology 65, 1329–1351. https://doi.org/10.1007/s00265-011-1195-1.

Pons, P., Rost, J., 2017. The challenge of conserving biodiversity in harvested burned forests. Conservation Biology 31, 226–228. https://doi.org/10.1111/cobi.12767.

Pons, P., Henry, P.-Y., Gargallo, G., Prodon, R., Lebreton, J.-D., 2003. Local survival after fire in Mediterranean shrublands: combining capture-recapture data over several bird species. Population Ecology 45, 187–196. https://doi.org/10.1007/s10144-003-0155-7.

Pons, P., Rost, J., Tobella, C., Puig-Gironès, R., Bas, J., M.,, Franch,, M.,, Mauri,, E.,, 2020. Towards better practices of salvage logging for reducing the ecosystem impacts in Mediterranean burned forests. iForest 13, 360–368. https://doi.org/10.3832/ifor3380-013.

Prodon, R., 2021. Birds and the Fire Cycle in a Resilient Mediterranean Forest: Is There Any Baseline? Forests 12, 1644. https://doi.org/10.3390/f12121644.

Prodon, R., Lebreton, J.-D., 1981. Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structure gradient. Oikos 37, 21–38. https://doi.org/10.2307/3544069.

Puig-Gironès, R., Real, J., Torre, I., 2022. A comprehensive but practical methodology for selecting biological indicators for longterm monitoring. PLoS One1 17 (3). https://doi.org/10.1371/journal.pone.0265246.

Puig-Gironès, R., Ferret, A., Rollan, À., Real, J., 2023a. Long-term response of open-habitats species to wildfire salvage logging: the endangered European wild rabbit as example. European Journal of Forest Research 142, 49–59. https://doi.org/10.1007/s10342-022-01504-1.

Puig-Gironès, R., Muriana, M., Real, J., Sabaté, S., 2023b. Unravelling the influence of annual weather conditions and Mediterranean habitat types on acorn production, availability and predation. Forest Ecology and Management 543, 121149. https://doi.org/10.1016/j.foreco.2023.121149.

Puig-Gironès, R., Pons, P., 2023. Mice population dynamics and structure over time and space after wildfires. Journal of Zoology. https://doi.org/10.1111/jzo.13101.

Puig-Gironès, R., Brotons, L., Pons, P., 2017. Aridity influences the recovery of Mediterranean shrubland birds after wildfire. PLoS One1 12, e0173599.

Puig-Gironès, R., Imbeau, L., Clavero, M., Rost, J., Pons, P., 2020. Does post-fire salvage logging affect foraging activity by rodents? European Journal of Forest Research 139, 777–790. https://doi.org/10.1007/s10342-020-01285-5.

Puig-Gironès, R., Brotons, L., Pons, P., 2022. Aridity, fire severity and proximity of populations affect the temporal responses of open-habitat birds to wildfires. Biological Conservation 272, 109661.

Puig-Gironès, R., Santos, X., Bros, V., 2023c. Long-interval effects of wildfires on the functional diversity of land snails. Science of The Total Environment 876, 162677. https://doi.org/10.1016/j.scitotenv.2023.162677.

R Development Core Team R: A Language and Environment for Statistical Computing In, R Foundation for Statistical Computing 2017 Vienna, Austria.

Retana, J., Espelta, J.M., Habrouk, A., Ordoñez, J.L., de Solà-Morales, F., 2002. Regeneration patterns of three mediterranean pines and forest changes after a large wildfire in northeastern Spain. Ecoscience 9, 89–97. https://doi.org/10.1080/11956860.2002.11682694.

Roberts, S.G., Thoma, D.P., Perkins, D.W., Tymkiw, E.L., Ladin, Z.S., Shriver, W.G., 2021. A habitat-based approach to determining the effects of drought on aridland bird communities. The Auk 138, ukab028. https://doi.org/10.1093/ornithology/ukab028.

Rodrigo, A., Retana, J., Picó, F.X., 2004. Direct regeneration is not the only response of mediterranean forests to large fires. Ecology 85, 716–729. https://doi.org/10.1890/02-0492.

Rost, J., Clavero, M., Bas, J.M., Pons, P., 2010. Building wood debris piles benefits avian seed dispersers in burned and logged Mediterranean pine forests. Forest Ecology and Management 260, 79–86. https://doi.org/10.1016/j.foreco.2010.04.003.

Rost, J., Hutto, R.L., Brotons, L., Pons, P., 2013. Comparing the effect of salvage logging on birds in the Mediterranean Basin and the Rocky Mountains: Common patterns, different conservation implications. Biological Conservation 158, 7–13. https://doi.org/10.1016/j.biocon.2012.08.022.

Saab, V.A., Russell, R.E., Dudley, J.G., 2009. Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. Forest Ecology and Management 257, 151–159. https://doi.org/10.1016/j.foreco.2008.08.028.

Santos, X., Bros, V., Miño, À., 2009. Recolonization of a burned Mediterranean area by terrestrial gastropods. Biodiversity & Conservation 18, 3153–3165. https://doi.org/10.1007/s10531-009-9634-2.

Schlossberg, S., 2009. Site fidelity of shrubland and forest birds. The Condor 111, 238–246. https://doi.org/10.1525/cond.2009.080087.

Stephenson, N.L., 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. Journal of Biogeography 25, 855–870. https://doi.org/10.1046/j.1365-2699.1998.00233.x.

Thorn, S., Bässler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L., Castro, J., Choi, C.-Y., Cobb, T., Donato, D.C., Durska, E., Fontaine, J.B., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R.L., Lee, E.-J., Leverkus, A.B., Lindenmayer, D.B., Obrist, M.K., Rost, J., Seibold, S., Seidl, R., Thom, D., Waldron, K., Wermelinger, B., Winter, M.-B., Zmihorski, M., Müller, J., Struebig, M., 2018. Impacts of salvage logging on biodiversity: A meta-analysis. Journal of Applied Ecology 55 (1), 279–289.

Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T.P., Donato, D.C., Durska, E., Macdonald, E., Feldhaar, H., Fontaine, J.B., Fornwalt, P.J., Hernández, R.M.H., Hutto, R.L., Koivula, M., Lee, E.-J., Lindenmayer, D., Mikusiński, G., Obrist, M.K., Perlík, M., Rost, J., Waldron, K., Wermelinger, B., Weiß, I., Żmihorski, M., Leverkus, A.B., 2020. Estimating retention benchmarks for salvage logging to protect biodiversity. Nature communications 11 (1). https://doi.org/10.1038/s41467-020-18612-4.

Thornthwaite, C.W., 1948. An Approach toward a Rational Classification of Climate. Geographical Review 38, 55–94. https://doi.org/10.2307/210739.

Tingley, M.W., Ruiz-Gutiérrez, V., Wilkerson, R.L., Howell, C.A., Siegel, R.B., 2016. Pyrodiversity promotes avian diversity over the decade following forest fire. Proceedings of the Royal Society B: Biological Sciences 283, 20161703. https://doi.org/10.1098/rspb.2016.1703.

Vallecillo, S., Hermoso Lopez, V., Possingham, H.P., Brotons, L., 2013. Conservation planning in a fire-prone Mediterranean region: threats and opportunities for bird species. Landscape Ecology 28, 1517–1528. https://doi.org/10.1007/s10980-013-9904-y.

Veraverbeke, S., Lhermitte, S., Verstraeten, W.W., Goossens, R., 2010. The temporal dimension of differenced Normalized Burn Ratio (dNBR) fire/burn severity studies: The case of the large 2007 Peloponnese wildfires in Greece. Remote Sensing of Environment 114, 2548–2563. https://doi.org/10.1016/j.rse.2010.05.029.

Watson, S.J., Taylor, R.S., Nimmo, D.G., Kelly, L.T., Clarke, M.F., Bennett, A.F., Gordon, I., Evans, D., 2012a. The influence of unburnt patches and distance from refuges on post-fire bird communities. Animal Conservation 15 (5), 499–507.

Watson, S.J., Taylor, R.S., Nimmo, D.G., Kelly, L.T., Haslem, A., Clarke, M.F., Bennett, A. F., 2012b. Effects of time-since-fire on birds: how informative are generalized fire-response curves for conservation management? Ecological Applications 22 (2), 685–696.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251. https://doi.org/10.2307/1218190.

Wood, S.N., 2017. Generalized additive models: an introduction with R. CRC Press, Bristol, UK.

S. Wood F. Scheipl gamm4: Generalized Additive Mixed Models using 'mgcv' and 'lme4'. R package version 0.2-6 2014 In, Vienna, Austria.

Zavala, M.A., Espelta, J.M., Retana, J., 2000. Constraints and trade-offs in Mediterranean plant communities: The case of holm oak-Aleppo pine forests. The Botanical Review 66, 119–149. https://doi.org/10.1007/bf02857785.

Zozaya, E.L., Brotons, L., Herrando, S., Pons, P., Rost, J., Clavero, M., 2010. Monitoring spatial and temporal dynamics of bird communities in Mediterranean landscapes affected by large wildfires. Ardeola 57, 33–50.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.