

Can predators influence small rodent foraging activity rates immediately after wildfires?

Roger Puig-Gironès^{A,B,*} 

For full list of author affiliations and declarations see end of paper

***Correspondence to:**

Roger Puig-Gironès
Departament de Ciències Ambientals,
University of Girona, C/Maria Aurèlia
Capmany 69, 17003 Girona, Catalonia,
Spain
Email: roger.puig.girones@gmail.com

ABSTRACT

Background. Habitat complexity, predation risk, and intraspecific competition shape rodent communities and impact foraging. Wildfires remove vegetation shelter, which increases the predation risk perception and leads to changes in trophic resources availability. Consequently, prey adjust their foraging activity levels to minimise the likelihood of encounters with predators. Rodents select safe habitats and can detect predators' scents, which allows them to reduce the predation risk when foraging. **Aims.** To evaluate the effects of carnivore occurrence and habitat structure on rodent foraging activity rates immediately after fires using mixed models and structural equation modelling. **Methods.** This study used 900-m linear transects to analyse environmental variables, acorn removal by rodents, and carnivore activity in three recently burnt areas. **Results.** In areas with higher stone marten abundances, rodents removed more acorns. However, acorn removal was also higher in structurally complex habitats with greater rodent abundance. **Conclusions.** Rodents' foraging activity is driven by increased interspecific competition and the predation risk perception due to the simplicity of the burnt habitat. Additionally, stone martens and rodents share the same preferences for habitat complexity after fires. **Implications.** Habitat complexity increases seed holding by rodents, which positively contributes to fire recovery and attracts predators, thereby increasing species diversity.

Keywords: carnivores, foraging activity, habitat structure, Mediterranean ecosystems, predator–prey interaction, rodents, seed dispersal, shelter, wildfires.

Introduction

Foraging activity is crucial to consumer fitness. Prey species adjust their foraging activity levels as a response to their predation risk, which represents the potential danger of being captured by a predator (Lima and Dill 1990; Houston *et al.* 1993). The availability of shelter and camouflage is a key determinant in prey foraging activity (Embar *et al.* 2011) because predator–prey encounters are relatively rare. The structure of the habitat, therefore, appears to be the main driver of the predation risk (Verdolin 2006). Small rodents are common prey items for a wide range of predators. Food availability determines the time required to obtain sufficient food, which in turn affects the risk of predator encounters because the cost of manipulating and carrying seeds can be high (Berger-Tal *et al.* 2009). For instance, the wood mouse (*Apodemus sylvaticus* L.), the most common small rodent in the Mediterranean Basin, selects safe habitats and microhabitats when foraging (Kotler *et al.* 2002; Díaz *et al.* 2005; Perea *et al.* 2011a). Shrubs typically provide shelter from predators and a place where rodents can forage and feed safely (Manson and Stiles 1998; Muñoz *et al.* 2009). Wood mice can also detect and respond to scents of predators such as the common genet (*Genetta genetta* L.), which further helps reduce the predation risk while foraging (Sunyer *et al.* 2013; Feldman *et al.* 2019). However, high levels of predation pressure at high-risk sites that lack shelter may lead to an increase in rodents' foraging efficiency (Chaby *et al.* 2015). The predation risk may also affect the choices made by wood mice: in more open high-risk conditions – as opposed to sites where there is good cover – mice preferred to remove larger acorns

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(Leaver and Daly 2003; Pérez-Ramos *et al.* 2008; Perea *et al.* 2011a). Intraspecific competitors, referring to individuals of the same species, have a significant influence on the foraging activity. In places where there is greater conspecific competition, it is expected that there will be an increase in foraging activity. This is because competition for resources intensifies individual foraging efforts to secure an adequate supply of food to maintain their fitness (Murray *et al.* 2006; Lichti *et al.* 2017).

Wildfires have an impact on faunal responses due to changes in habitat structure, direct mortality and greater predation risk (Morris *et al.* 2011; He *et al.* 2019). Fires modify predator–prey interactions by altering food availability and habitat structure, and thus influence predation rates (Persson and Eklov 1995; Janssen *et al.* 2007) and foraging activity (Vander Wall 2010; Conner *et al.* 2011; Perea *et al.* 2011b; Leahy *et al.* 2016; Morán-López *et al.* 2016). Burnt areas lead to changes in prey abundance, distribution, and behaviour, and affect predators' diets (Doherty *et al.* 2022). Predators with flexible diets can exploit changes in prey availability by targeting more profitable species in terms of availability and ease of capture (Perea *et al.* 2011a). After fire in south-eastern Australia, the red foxes (*Vulpes vulpes* L.) exhibited a two-fold increase in consuming medium-sized native mammals, and their preference for long-nosed bandicoots (*Perameles nasuta* Geoffroy) and short-beaked echidnas (*Tachyglossus aculeatus* Shaw) also increased (Hradsky *et al.* 2017a). Predators can affect prey directly if they are attracted to burnt areas, or indirectly through changes in habitat structure (McGregor *et al.* 2016; Puig-Gironès and Pons 2020; Doherty *et al.* 2022). Certain prey species may benefit from habitat openness, which will enable them to detect and avoid predators more easily (Cherry *et al.* 2018), whereas others require denser cover to reduce the predation risk (Perea *et al.* 2011a; Doherty *et al.* 2015). Numbers of certain prey species (such as wood mice) increase in burnt areas following plant recovery (Monimeau *et al.* 2002; Torre and Díaz 2004) because they are able to find more resources and competition is less severe compared with unburnt areas (Puig-Gironès and Pons 2023). However, prey species may use sites with structurally complex habitats or make convoluted movements when foraging as a result of heightened predation risk (Fordyce *et al.* 2016; Lees *et al.* 2022). Habitats that provide cover, such as piles of wood debris, can create shelter for prey species (Puig-Gironès *et al.* 2020). On the other hand, animals under predation risk may be more selective and drop low-profit items from their diet, or be less selective because selectivity demands more extensive foraging activity and greater exposure to risk (Leaver and Daly 2003; Chaby *et al.* 2015).

The 'oak-wood mouse–common genet' model has been well studied because the genet is the most specialised predator of mice in Mediterranean forests (Virgós *et al.* 1999; Díaz *et al.* 2005; Rosalino *et al.* 2011; Sunyer *et al.* 2013; Feldman *et al.* 2019). However, the common genet appears

to be rare in Mediterranean burnt areas (Birtsas *et al.* 2012; Puig-Gironès and Pons 2020). Nevertheless, stone martens (*Martes foina* (Erxleben, 1777)) and red foxes may take advantage of the higher abundance of mice and lower availability of shelter in such areas. The former is a territorial species that prefers areas with well-developed tree cover (Vergara *et al.* 2016). However, it is positively attracted to recently burnt areas, especially when the habitat structure is complex (Puig-Gironès and Pons 2020), which matches the habitat preferences of rodents. The stone marten has a wide-ranging diet that is well adapted to the availability of local resources. Its main food items consist of small mammals and, particularly, fleshy fruits (Baghli *et al.* 2002; Rosalino and Santos-Reis 2009). Red foxes may also predate on small rodents. However, despite their preference for open habitats, fox abundances could affect the foraging activity of rodents that choose preferentially denser cover (Manson and Stiles 1998; Muñoz *et al.* 2009; Puig-Gironès *et al.* 2018; Puig-Gironès and Pons 2020).

The aim of this study was to describe the possible effects of predator occurrence (stone martens and red foxes) on small rodent foraging activity rates (hereafter 'SRFAR') in three recently burnt forests in Catalonia (W Mediterranean Basin). It was predicted that the presence of predators would increase rodents' predation risk directly, due to their physical presence, and indirectly via cues such as scents and faeces (Herman and Valone 2000). Accordingly, the following hypotheses and predictions were generated: (1) stone marten occurrence will increase rodents' predation risk and modify their foraging activity rates; (2) red fox occurrence will not significantly affect rodent foraging rates in burnt areas because their utilisation differs between the two species (Birtsas *et al.* 2012; Puig-Gironès and Pons 2020); (3) rodent foraging rates will be higher in areas with greater shrub cover, and their foraging activity will increase in concert with time since fire due to greater habitat complexity (Muñoz *et al.* 2009; Perea *et al.* 2011b; Puig-Gironès *et al.* 2018); and (4) foraging activity rates will be reduced with increasing distance from shelter, and resources further from shelter will be utilised less frequently due to higher predation risk. Therefore, shelter such as shrubs or piles of woody debris will provide a release from predation pressure and promote increased foraging activity in recently burnt habitats (Puig-Gironès *et al.* 2020).

Material and methods

Study area

Three recent (less than 6 months beforehand) severely burnt areas (over 200 ha) in Catalonia (NE Iberian Peninsula; Fig. 1) were studied. Two of the study areas (La Jonquera and Rasquera) were located in lowlands with Mediterranean climate and one (Ger) in the Pyrenees with a humid Mediterranean climate. All sites were studied for 30 months

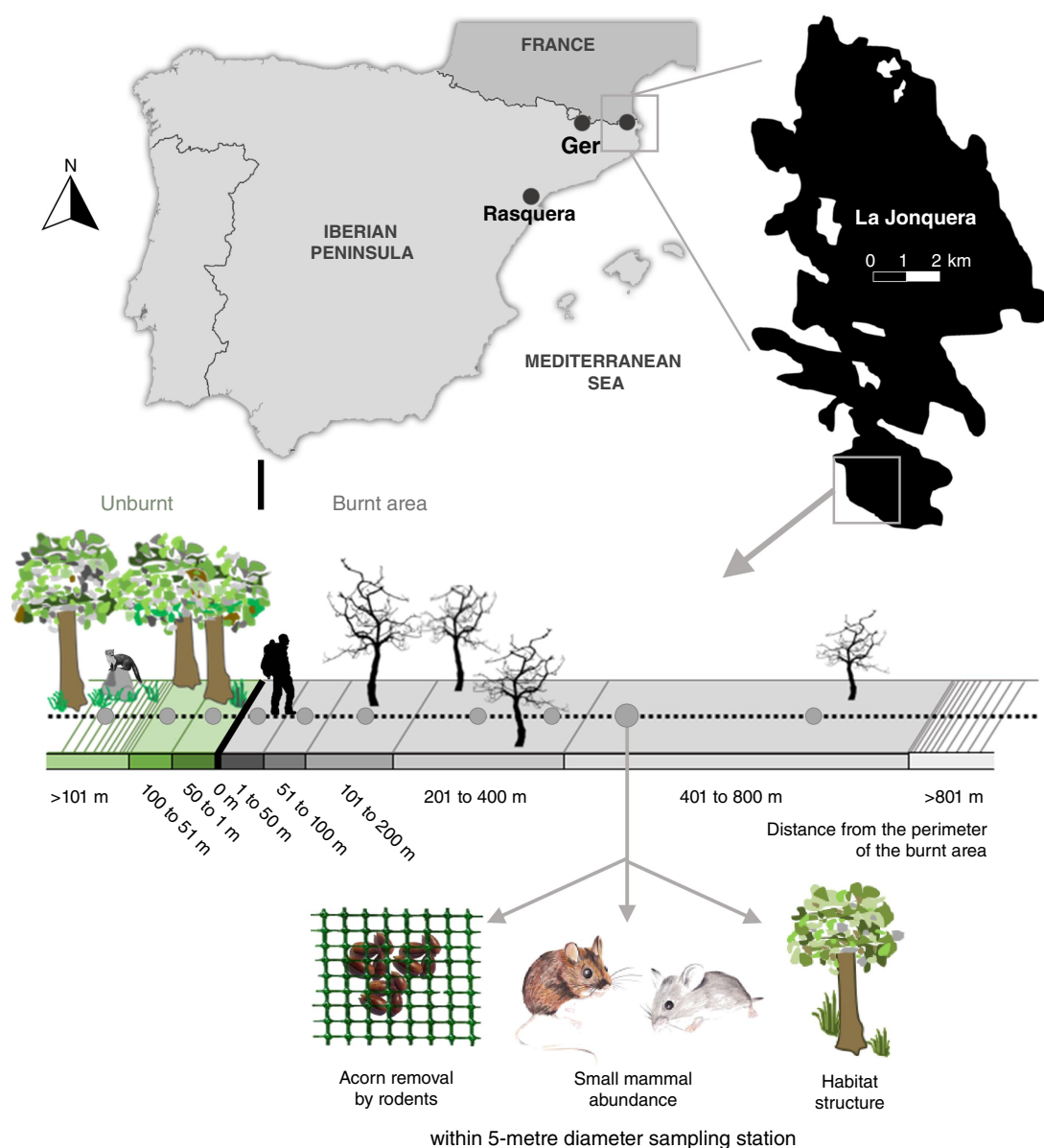


Fig. 1. Location and schematic representation of the sampling methods. Location of the three burnt study areas (La Jonquera, Ger and Rasquera) in Catalonia (NE Iberian Peninsula), using the La Jonquera burnt area as an example in black, and schematic representation of linear transects, perpendicular to the burnt area perimeter with sampling stations (grey dots) at increasing distances from the burnt area perimeter. In each sampling station of 5 m diameter, I measured acorn removed by rodents (with an acorn device), the relative abundance of rodents (with a Sherman live trap), and habitat structure (plant cover and height, herbaceous cover and height (as opposed to woody)).

after fires. Their main characteristics are given in Table 1, and more information on the study sites can be found in Puig-Gironès *et al.* (2018).

Sampling design and field methods

To collect data on SRFAR and carnivore activity (hereafter 'signs'), linear transects (approximately 900 m long and 10 m wide) were established in each study area. Transects were placed perpendicular to the linear edge of the burnt area

(Table 1, Fig. 1) to avoid any influence of border geometry on edge effects (Fernández *et al.* 2002). Both burnt and unburnt areas were included in the transects. Nearby transects were located, on average, $2048 \text{ m} \pm 540 \text{ s.e.}$ from each other, with a minimum distance of 250 m at the closest point. In all, 61% of nearby transects were separated by at least 500 m, a distance that ensured that there was reasonable spatial independence to avoid double counts.

To survey carnivore activity, the observer slowly walked each transect and, within a 3-m-wide band on each side of

Table 1. Characteristics of the four burnt areas.

Wildfire	La Jonquera	Rasquera	Ger
Region	Mediterranean	Mediterranean	Pyrenees
Bioclimate	Subhumid Mediterranean	Dry continental Mediterranean	Humid Mediterranean mountain
Altitude min/average/max (m)	90/263/574	317/348/409	1461/1672/1893
Burnt area (ha)	13088	3082	250
Date of burnt	August 2012	May 2012	August 2012
Time after fire in first sampling (weeks)	2	18	1
Last sampling week	117	138	118
Pre-fire habitat	Oak, pine and shrubland	Pine and shrubland	Pine and shrubland
Number of transects	9	5	11
Sampling occasions	15	7	16
Number of stations	Unburnt	15	33
	Burnt (including perimeter)	63	77

Description of the four burnt areas sampled for 2.5 years. The number of burnt stations includes the station located on the burnt area perimeter (for more information see Puig-Gironès *et al.* 2018).

transect, looked for signs (faeces) (Fig. 1). For each sign found, the species was determined, UTM coordinates were noted, and the faeces were removed from transect. Field signs did not allow us to estimate carnivore abundance due to differences in species detectability caused by their particular ways of marking the territory. Nevertheless, given that red foxes and stone martens deposit their faeces in clearly visible places, field signs could be used as a proxy of carnivore activity at species level (see Ruiz-Capillas *et al.* (2013)).

Predators have great territorial mobility but low-density populations, so each transect was divided into two categories in terms of the *distance from the burnt area perimeter* and eight further categories in terms of the *time since fire* to maximise the information derived from detected stone marten signs. Negative *distance from the burnt area perimeter* values were assigned to points within the unburnt area ($-1 = 1\text{--}50\text{ m}$; $-2 = 51\text{--}100\text{ m}$; and $-3 = \text{over } 100\text{ m}$ from the burnt area perimeter), whereas positive values indicated distances within the burnt area ($0 = 0\text{ m}$; $1 = 1\text{--}50\text{ m}$; $2 = 51\text{--}100\text{ m}$; $3 = 101\text{--}200\text{ m}$; $4 = 201\text{--}400\text{ m}$; $5 = 401\text{--}800\text{ m}$; and $6 = \text{over } 800\text{ m}$ from the perimeter). The *time since fire* values were grouped into monthly categories ($1 = 1\text{--}2\text{ months}$ after fire; $2 = 3\text{--}4$; $3 = 5\text{--}6$; $4 = 7\text{--}10$; $5 = 11\text{--}15$; $6 = 16\text{--}20$; $7 = 21\text{--}25$; and $8 = 26\text{ months}$ from the end of the sampling period).

Each transect was visited a minimum of seven and maximum of 16 times. At La Jonquera and Ger, the sampling frequency decreased with time after the fire, being monthly in the first 6 months, bimonthly at 7–24 months, and every 3 months thereafter until 30 months had elapsed since the fire. This variation in the sampling frequency during the

study ensured that all of the most relevant information regarding the recolonisation process was gathered. Indeed, small rodents are known to be early colonisers (Sainz-Elize *et al.* 2012; Puig-Gironès *et al.* 2018), and it was therefore important to sample more intensely during the first months after fire. Rasquera was, however, sampled constantly every 3 months starting 18 and 23 weeks after fire, respectively (Table 1).

Along each transect 10 5-m-diameter rodent–vegetation sampling stations were established, three in the unburnt area (at approximately 25, 50, and 100 m from the perimeter of the burnt area), one on the perimeter of the burnt area, and six inside the burnt area (at 25, 50, 100, 200, 400, and 800 m from the perimeter) (Fig. 2). At each sampling station, the SRFAR, rodent relative abundance, and other environmental variables (Fig. 1) were measured. The acorns removed by rodents were taken to be a surrogate of SRFAR because acorns are easy to collect and naturally available in and/or near the study sites, and are positively selected by small rodents (Pons and Pausas 2007). The devices offering acorns to rodents (henceforth, ‘acorn devices’) were placed in the centre of each sampling station and consisted of a $50 \times 50\text{-cm}$ meshed cage (1.27 cm^2 mesh size) containing 20 cork oak (*Quercus suber* Linnaeus, 1753) acorns. The acorn devices were always installed in the same places, generally below shrubs or, if not possible, very close (less than 20 cm) to shrubs, herbs, or a stone wall to minimise the microhabitat effect on removal. Each device had four small entrances ($5 \times 5\text{ cm}$) that prevented jays (*Garrulus glandarius* (Linnaeus, 1758)) and other birds from entering. The cork oak acorns were all of similar sizes ($2.5 \pm 0.2\text{ cm}$ in length; mean $\pm$ s.e.) to avoid any effect of acorn size on the

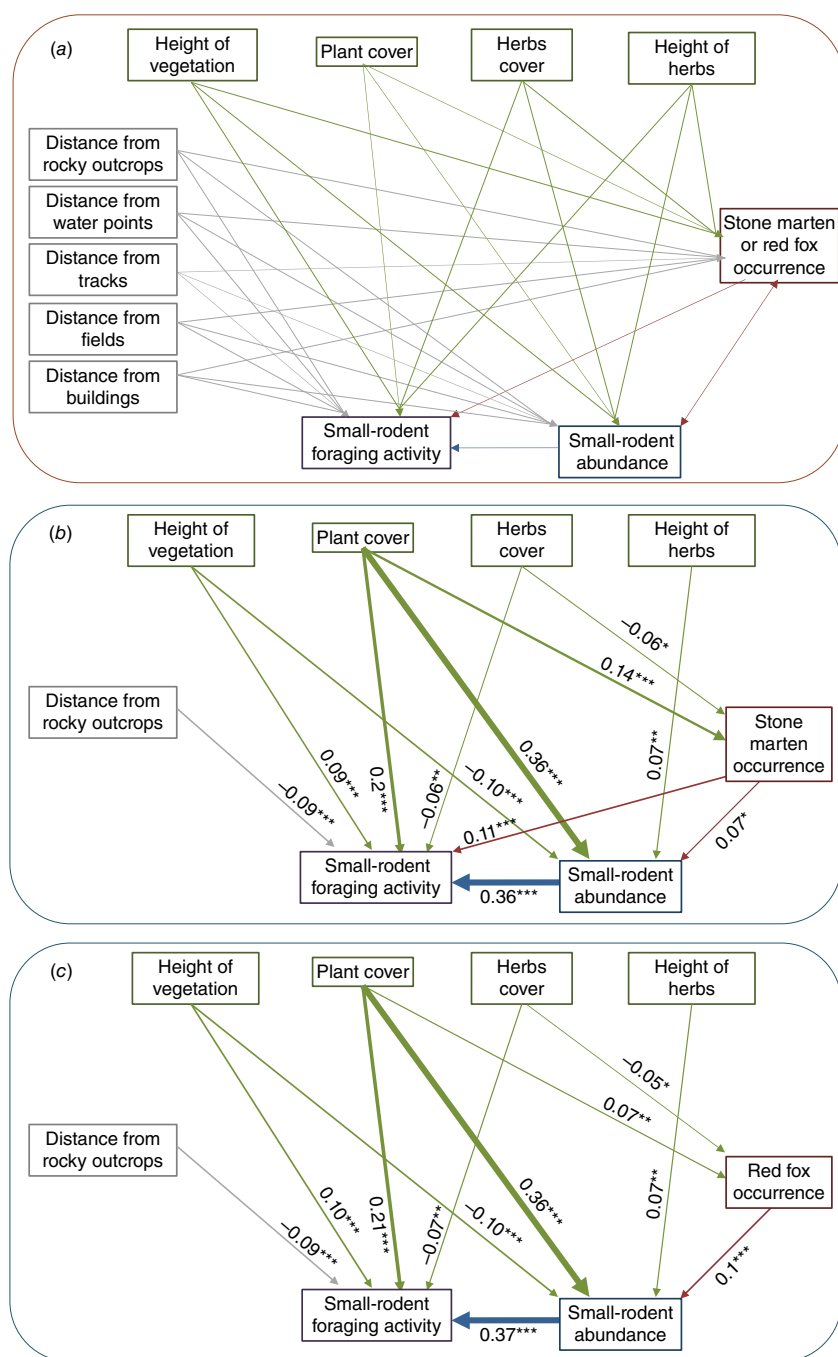


Fig. 2. Most Parsimonious Structural Equation Models (SEM). (a) All paths in the initial models were treated as optional and were thus able to be removed during model simplification (from 31 to 14 parameters) using maximum likelihood estimation. (b and c) As a final model, I selected the model with the lowest AICc score. One-way arrows represent paths between variables. Values adjacent to paths indicate standardised direct coefficients, with significance indicated by *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

removal probability. All acorns, collected from cork oak forests near the study area at La Jonquera, were externally analysed to rule out arthropod perforations and then conserved in a dry freezer.

A Sherman live trap for small mammals ($5.1 \times 6.4 \times 22.3$ cm, Sherman, Tallahassee, Florida, USA), placed in the centre of each sampling station, was baited with a mixture of tuna, flour, oil, and a piece of apple (Torre and Díaz 2004) and thermally protected. Sherman traps were placed following the criteria used for the acorn devices. Captured small mammals were identified to species level,

sexed, and marked with ear tags (National Band Co., USA). All sampling procedures met ASM Care & Use guidelines (Sikes *et al.* 2011). Three rodent species were live-trapped: wood mouse; Algerian mouse (*Mus spretus* Lataste, 1883); and common vole (*Microtus arvalis* (Pallas, 1778)). In subsequent analyses, rodent abundance was used as a proxy for interspecific competition among rodents. Acorn devices and Sherman traps were installed alternatively at sampling stations to avoid interference between devices. They were checked on the first day after installation, and the Sherman traps were used to capture rodents on three

consecutive mornings after installation. In this way, each sampling station was active for a minimum of 4 days during each sampling event.

The habitat structure and the dominant vegetation type (herbaceous or woody/shrub) were sampled on each sampling occasion and at each 5-m sampling station concurrently with the sampling of the animal population. Habitat structure was characterised at each sampling station using the following measurements: foliage cover (%), an indicator of vegetation recovery, was estimated using a reference chart for six virtual vegetation height layers: 0–0.25 (C0); 0.25–0.5 (C25); 0.50–1 (C50); 1–2 (C100); 2–4 (C200); and >4 m (C400) (Prodon and Lebreton 1981). A principal component analysis (PCA) was then used to summarise the information obtained from the six variables after arcsine-transforming cover values. The first component (henceforth *plant cover*; 42.6% of explained variance) corresponded to the extent of plant cover, and the second (henceforth *height of vegetation*; 27.9% of explained variance) ranked stations in terms of the height of the dominant vegetation layers (Supplementary File S1a). Also, the cover percentage of woody species was estimated at three height layers, 0–0.25, 0.25–0.5, and 0.50–1 m, which was the inverse of the proportion of the herb or non-woody species foliage cover. A principal component analysis (PCA) was used to summarise the information in which the first component (henceforth *herb cover*; 54% of explained variance) corresponded to the extent of the herb species foliage cover, and the second (PC2, henceforth *height of herbs*; 28% of explained variance) ranked stations in terms of the maximum height of the herb cover (Supplementary File S1b). These four components of the habitat structure and plant dominance (plant cover, height of vegetation, herb cover, and height of herbs) were used as independent variables in the analyses.

The possible role of other potential shelters for fauna was characterised by measuring their distance from the centre of the sampling stations in the burnt area. Rocky outcrops or piles of stones (*distance from rocky outcrops*), water sources (ponds, streams, etc.; *distance from water*), rural constructions (dry-stone walls, farmhouses, barns, etc.; *distance from buildings*), tracks and paths (*distance from tracks*), and cropland (both active and abandoned; *distance from fields*) were also regarded as potential shelters.

Finally, 25 sampling stations along seven transects were selected in a burnt area where a post-fire treatment involving the creation of piles of woody debris had been performed. The sampling stations were randomly selected, with preference given to those with well-built piles. At each sampling station, an acorn device and a Sherman trap were set up in three places: (1) underneath the pile; (2) 5 m from the pile; and (3) 10 m from the pile (see Puig-Gironès *et al.* (2020) for more details about logging process). The sampling of these piles was conducted at the Ger study area simultaneously with the sampling of the unlogged transects (15 occasions, at 5–118 days after fire).

For each sampling station (pile-centred), the exact distance was measured from the burnt area perimeter, as was the foliage cover (%) of the two virtual vegetation height layers (0–0.25 (C0) and 0.25–0.5 (C25)) and the rock cover. The woody debris piles were considered as potential shelter in areas with little cover in order to test the effect of shelter availability after fire on foraging rates under varying predation risk.

Statistical analyses

I used the proportion of the maximum number of acorns that could potentially be removed (limited to 20 acorns per sampling event) on the first night after the installation as a surrogate for the acorns removed by rodents, i.e. the foraging activity. A single night of acorn removal was used to avoid the possible throw-off foraging rate produced by discovering a source of abundant food on the first night. Therefore, SRFAR refers to the proportion of acorns removed by rodents. Signs (faeces) were used as occurrence at each transect and visit (0–1) for both red foxes and stone martens, given the heterogeneity of their detectability due to their habit of marking their territories and the transect habitat structure. Because a maximum of three rodents could be trapped per sampling event (three consecutive nights), the proportion of this number caught was used as a surrogate of rodent abundance, so ‘relative abundance’ refers to the proportion of traps occupied by rodents (0, 0.33, 0.66 or 1).

Mixed models were used to assess the importance of predator presence, habitat, and shelter on SRFAR. To evaluate the predation risk on rodents, a general linear mixed model (GLMM) was used to analyse the effects of *red fox occurrence* and *stone marten occurrence* on acorns removed by rodents. In addition, for each analysis, variables derived from habitat structure (*plant cover*, *height of vegetation*, *herb cover*, and *height of herbs*), variables related to fire (the categories of *distance from the burnt area perimeter* and *time–distance interaction*), variables describing shelter (*distance from rocks*, *water*, *buildings*, *tracks*, and *fields*), and variables describing interspecific competition (*rodent abundance*) were incorporated as fixed factors. The particular *Transect* was included as random factor to control possible site-based differences and temporal pseudo replication. Rodent abundance can be a confounding variable for carnivores, habitat structure, and rodent foraging rates, so rodent abundance was added as a random variable (random slope) to avoid any possible masking of the real relationship between the other variables. Random assignment minimises the effects of confounding variables by distributing them equally among all the experimental groups. Finally, the GLMM was used to test the effects of the microhabitat (shelter) on (1) one night, (2) three nights after the acorn device installation, and (3) rodent abundance. Here, the distance to shelter, distance from the burnt area perimeter, time since fire, the foliage cover (%) of 0–0.25 (C0) and

0.25–0.5 (C25), and the cover of rocks were used as fixed factors.

A multi-model inference approach was used to select the most important variables based on all possible sub-models developed from the acorn removal explanatory variable. Before model analysis, data were tested for multicollinearity diagnostics (Zuur *et al.* 2009) and variability (outliers) (Zuur *et al.* 2010). A check for multicollinearity was performed by quantifying variance-inflation factors (VIF) and generalised variance-inflation factors (GVIF[1/(2df)]), which were calculated for each fixed factor (Fox and Monette 1992). Large VIF or GVIF values (arbitrary threshold of ≤ 2.5 suggesting collinearity) were sequentially dropped from further analysis. However, no collinearity was found between variables. All possible models were then ranked according to their Akaike Information Criteria corrected for small samples (AICc) (Burnham and Anderson 2002). From the set of variables selected, all the possible combinations of the predictor variables (described above) generating different biologically meaningful models were explored. For each model, the AIC weight (AIC ω) was calculated (total AIC ω adds 1) (Wagenmakers and Farrell 2004). Furthermore, if there was no clear most-parsimonious model (i.e. one or more models with an AICc difference less than 2 from the best model), the average final model was estimated from all the models (Burnham and Anderson 2002). The weight of each variable in the average final model – the AIC weight (ω_i) – was calculated as the relative variable importance (Supplementary Table S1). To interpret the magnitude of each variable in the average final model, the relative importance of each variable (RVI) was weighted based on the sum of ω_i for each variable. The RVI ranges from 0 to 1, so the explanatory variable was considered robust if it had an RVI > 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 (Kennedy *et al.* 2013; Chiaradia *et al.* 2016). Additionally, if standard errors (s.e.) were large ($1.96 \times \text{s.e.} > \text{parameter appreciation}$), the estimate of the parameter was considered imprecise and was removed from the final model. To perform these analyses, R software (R Development Core Team 2017) with the *lme4* (Bates *et al.* 2015) and *MuMIn* (Bartoń 2016) packages was used.

Although the above-described GLMM checked the effects of the initial hypotheses, it was also possible that acorn removal depended on another variable or was affected by a series of complex indirect effects. Therefore, to control for these possible indirect and confounding variables, structural equation modelling (SEM) was used with the R package *Lavaan* (Rosseel 2012) to distinguish between potential causal pathways and to control for possible indirect effects. To reduce SEM complexity and for each system, two initial (maximal) models (Fig. 2a) were constructed with a variety of pathways allowing for (1) stone marten occurrence or (2) red fox occurrence and environmental and temporal variables to affect the SRFAR. All paths in the original model

were treated as optional and could thus be removed during model simplification. Non-significant terms were removed until the model fit (assessed using Akaike Information Criterion) no longer improved. When the model fit did not differ significantly between two competing models (i.e. the difference in the AICc score was < 2), the most parsimonious (the model with the fewest parameters) and the most appropriate models were selected (Supplementary Table S2). The appropriateness was assessed by employing the greater comparative fitness index (CFI values greater than 0.95), the root means square error of approximation (RMSEA less than 0.08), and the standardised root mean square residual (SRMR less than 0.08) criteria (Hu and Bentler 1999; Hooper *et al.* 2008). The CFI is an incremental fitness index that compares the fitness of a hypothetical model with that of a baseline model (i.e. the model with the worst fit). Conversely, RMSEA is an absolute fitness index, because it assesses how far a hypothesised model is from a perfect model. SRMR is a standardised effect size of the overall misfit suitable for covariance structure models.

Animal Ethics

All sampling procedures met the ASM Care & Use guidelines (Sikes *et al.* 2011).

Results

Of all the carnivores, the red fox and stone marten were the most common species in the studied areas; genet, European badger (*Meles meles* Linnaeus, 1758) and least weasel (*Mustela nivalis* Linnaeus, 1766) were also present, albeit in much smaller numbers (Puig-Gironès and Pons 2020). During the study, 196 signs (faeces) of red fox (111) and stone marten (85) were detected, 7050 acorns (11.1% of the total number supplied) were removed by rodents on the first night after acorn supply (2.22 ± 0.14 mean ($\pm$ s.e.) acorns removed per site and night) and 902 rodents were captured (74.7% of which were wood mice, 20.3% Algerian mice, and 5% common voles).

Time since fire, plant cover, rodent abundance, and stone marten occurrence were the principal factors explaining SRFAR. Rodent abundance had the largest standardised total effect on SRFAR, and plant cover had the second-largest effect on the structural equation model (SEM) (Fig. 2). Stone marten occurrence had a significant positive effect on acorn removal rates by rodents (Fig. 2b), and red fox occurrence had no effect on SRFAR. Both predators also indirectly affected removal rates (Supplementary Tables S3, S4), which were mediated positively by rodent abundance and plant cover. On the other hand, other habitat variables such as height of vegetation, distance from rocky outcrops, and herb cover affected the number of acorns removed by rodents. The rate of acorn removal from the

Table 2. Effect of environmental variables on rodent foraging activity rates.

Explanatory variables	Coefficient	Standard error	t-value	P-value	RVI
Intercept	0.14	0.010	10.19	<0.001	
Time since fire	0.01	0.002	6.08	<0.001	1.00
Plant cover	0.04	0.004	10.27	<0.001	1.00
Rodent relative abundance	0.46	0.030	5.34	<0.001	1.00
Stone marten occurrence	0.09	0.030	2.53	0.010	0.42

Summary of the selected model, derived from generalised linear mixed models (GLMM) analyses of number of acorns removed by rodents. The table shows the model parameter coefficient, its standard error ($\pm$ s.e.), and the associated t-value and P-values. The relative importance of each variable (RVI) ranges from 0 to 1, so 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. *Intercept* is the value of acorns removed by rodents when all the covariates are = 0, and P-value indicates whether it is significantly different from 0.

acorn device decreased at greater distances from shelter such as rocky outcrops. Although plant cover and height of vegetation increased over time, herb cover and height stopped increasing after 7 months and remained stable thereafter (Supplementary Fig. S1). Removal rates were especially high immediately after fire, when the availability of natural resources was practically null.

Although general linear mixed models (GLMM) showed that the greater the presence of martens, the higher the rates of acorn removal (Table 2), this effect did not seem to be sufficient or relevant (RVI less than 0.5) in the model. Furthermore, the presence of red foxes did not affect rodent foraging rates. However, a more complex habitat structure (plant cover) also prompted greater rates of acorn removal by rodents. The number of acorns removed varied in terms of the time since fire, with a notable increase in acorn removal immediately after fire to 2.5 years afterwards. In addition, a greater abundance of rodents implied that more acorns were removed (Fig. 3).

Finally, the experimental woody debris piles showed that the variables of distance to shelter and foliage cover between 25 and 50 cm (Supplementary Table S5) were the most effective in explaining foraging activity by rodents and the positive effects of protection associated with the predation risk immediately after fire. Specifically, both variables had a significant positive effect on acorn removal one and three nights after installation and on rodent captures (Fig. 4).

Discussion

The results identified a relationship between acorn removal by rodents and stone marten occurrence, thereby suggesting that this predator has the capacity to influence rodent foraging activity rates, which would lead us to accept the first hypothesis. Removal rates suggest that rodents select high-profitability items (acorns), spend less time exploring for food, and have greater urgency when food collecting if they have a higher danger (Leaver and Daly 2003; Chaby *et al.* 2015; Lichti *et al.* 2017). However, acorn removal increased over time where the habitat was structurally more

complex because higher abundances of mice find cover in such habitats (Fordyce *et al.* 2016; Puig-Gironès *et al.* 2018; Lees *et al.* 2022). Conversely, this may also attract more stone martens to burnt areas (Puig-Gironès and Pons 2020; Doherty *et al.* 2022). In this sense, the importance of microhabitats for foraging in habitats in the experiment immediately after fires was clear. In areas with bare ground, the presence and proximity of protection is key, as has been reported by other authors (Ceradini and Chalfoun 2017; Crego *et al.* 2018; Abdulwahab *et al.* 2019). Moreover, the results show that the presence of red foxes did not affect acorn removal by rodents, as predicted in the second hypothesis. Accordingly, it could be argued that foraging activity by rodents after fires could be driven by both the direct and indirect effects of predation (i.e. by the direct presence of predators) and by the predation risk due to the scarcity of shelter and the simplicity of the burnt habitat (although that was not explicitly measured in this study).

Small mammals can detect and recognise signs that betray the presence of carnivores, so their responses to predators will vary depending on the direct risk of being captured or on indirect factors such as the quality of the available shelter or amount of moonlight (Perea *et al.* 2011a; Sunyer *et al.* 2013; Hegab *et al.* 2014). Stone martens are regular consumers of small mammals, which represent about 30–35% of their diets (Ballesteros *et al.* 2000; Padial *et al.* 2002). They probably take advantage of burnt areas to increase the frequency of rodents in their diet, as has been shown in other carnivores (Doherty *et al.* 2022). Thus, stone marten occurrence in burnt areas may force rodents to spend less time foraging to avoid increasing their exposure to predation (Brown 1988) and oblige them to select positively high-profitability acorns (McMahon *et al.* 2018). The presence and proximity of shelter (such as shrub cover or rocky outcrops) are very important factors that interact and affect rodent foraging activity rates. In addition, the ability of wood mice to hoard acorns may potentially affect acorn removal rates if acorn devices are placed near suitable storage locations. Consequently, greater predation risk may also increase acorn removal; i.e. wood mice will remove acorns sequentially and store them in a more

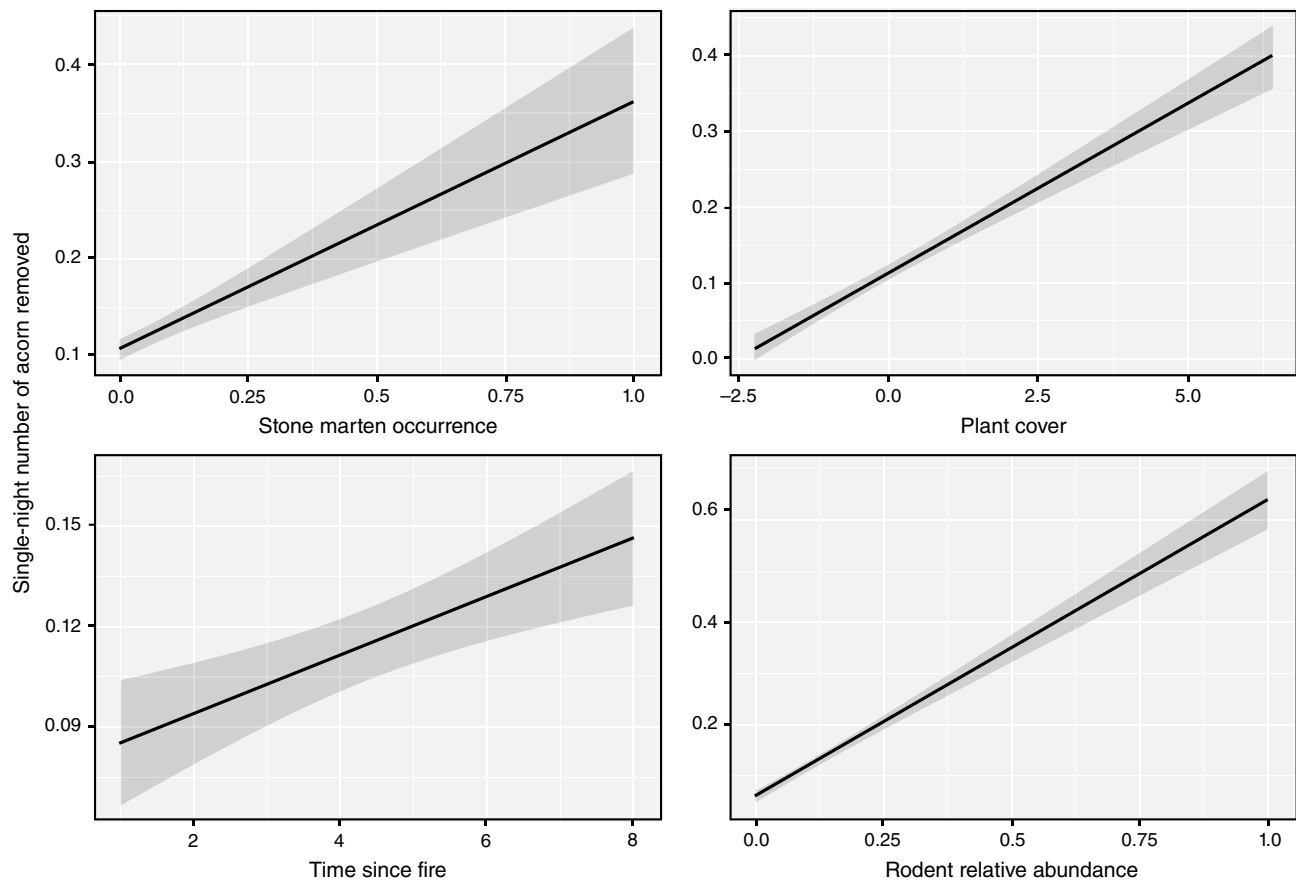


Fig. 3. Model predictions of variables over rodent acorn removal rates. Marginal effects (measuring the instantaneous rate of change) of the model predictors on rodent foraging activity rates according to stone marten occurrence, plant cover, time since fire, and rodent relative abundance. Trend line and standard error shown were obtained from GLMM model estimates.

secure location for later consumption. By contrast, Algerian mice tend to store acorns, often beyond the vegetation canopy when pilferage rates are low and if seed availability is low and competitors are abundant (Muñoz and Bonal 2011). Consequently, higher acorn removal may be due to increased foraging activity associated with higher rodent abundance, so predation by stone martens may not in fact be the key driver of the fate of seeds, as is suggested by the structural equation model (SEM). Additionally, the positive relationship between stone martens and acorn extraction rates is probably due to the spatial distribution of stone martens relative to mice distribution (Vergara *et al.* 2016; Puig-Gironès and Pons 2020). This may also explain why the risk of predation by foxes did not influence foraging rates by rodents. Foxes were more abundant in the study areas due to their preference for open habitats (Hradsky *et al.* 2017b; Puig-Gironès and Pons 2020).

The type of shelter (vegetation or rocks) affected foraging activity: stations with appropriate herb cover had lower acorn removal rates, lower rodent abundance and lower stone marten occurrence. By contrast, in places with shrub cover, rodent activity increased as predicted and has been

reported in other studies (Smit *et al.* 2008). Immediately after fire, acorn removal activity was higher as a reaction to a scarcity of resources and the increased perception of the predation risk due to the lack of plant cover. Wood mice have a preference for dense shrub cover when conditions are unfavourable (Ouin *et al.* 2000), which affords protection and shelter (Díaz 1992). These results are thus similar to those for fragmented forests, in which a more complex habitat structure is the main driver of prey-foraging decisions (Morán-López *et al.* 2015). Low shelter availability minimises prey movements, and the interplay between intra-specific competition and predation risk has important effects on caching rates (Vander Wall 2010; Perea *et al.* 2011b; Morán-López *et al.* 2016). Therefore, post-fire habitat structure, microhabitats, and the predation risk affect rodent foraging activity (Conner *et al.* 2011; Leahy *et al.* 2016) and draw predators to burnt areas if prey is abundant and vulnerable to predation (McGregor *et al.* 2016). Throughout Catalonia, rodent foraging activity increased considerably in burnt areas 15 months after fire (Puig-Gironès *et al.* 2018, 2020). However, although rodent numbers remained high in burnt areas in the first weeks after fire, a lack of plant

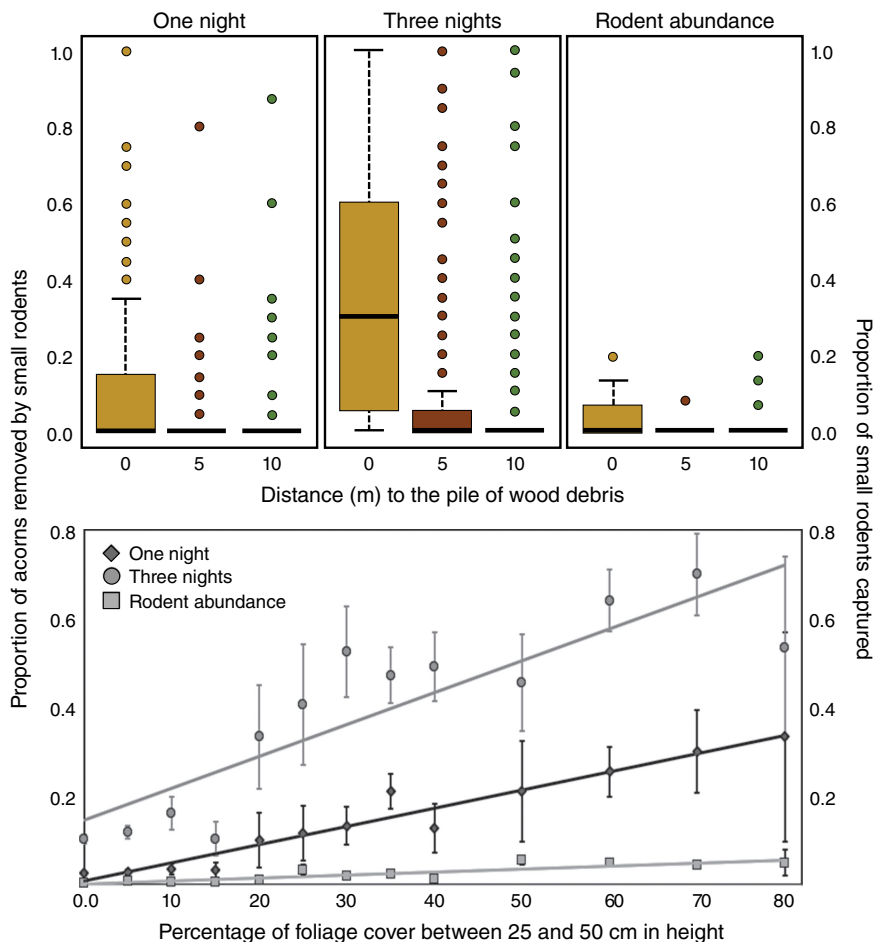


Fig. 4. Acorn removal and rodent abundance over distance to shelter. The number of acorns removed by rodents (a) one night, (b) three nights after offering, and (c) the proportion of rodent abundance depending on the distance to the shelter (wood debris pile): below, at 5 m and at 10 m, and on the percentage of foliage cover between 25 and 50 cm in height are shown.

cover may slow down the colonisation by stone martens. Immediately after fire, stone martens frequented the perimeter of the burnt areas (Puig-Gironès and Pons 2020), where refuges and food resources were more available (Puig-Gironès *et al.* 2018). In conclusion, the results seem to indicate that in the study area, rodents reacted to the perception of the predation risk rather than to the occurrence of predators, and that stone martens and rodents have similar habitat preferences.

The increase in rodent abundance over time and the quantity of shelter (due to habitat complexity) lead to an increase in competition for resources and ultimately an increase in acorn removal rates. Functional responses of rodents are influenced by resource availability, as well as by the relative abundances of different seeds and competitors (Murray *et al.* 2006; Klinger and Rejmánek 2009; Ostoja *et al.* 2013). Foraging and hoarding locations may also vary spatially and temporally as a function of habitat structure, competition, perceived predation risk, and pilferage risks (Pérez-Ramos *et al.* 2008; Muñoz *et al.* 2009; Muñoz and Bonal 2011; Perea *et al.* 2011b). However, such competition may not benefit plant regeneration, because less-intense competition and less pilferage pressure may lead hoarders

to invest less heavily in seed transport, thereby resulting in lower rates of seed dispersal (Murray *et al.* 2006).

Implications

This study focused on the foraging activity rates of rodents under natural conditions. Seed removal plays an important role in the dispersal mechanisms of animal-dispersed plants. Thus, the rodent foraging decision-making process may be fundamental in animal-mediated seed dispersal in burnt areas. Consequently, the presence of predators may alter seed dispersal rates by prey items (Xiao *et al.* 2005) and thus have implications for post-fire plant and ecosystem regeneration. The wood mouse is a pioneer species in burnt habitats, which it recolonises from unburnt and ecotone areas (Torre and Díaz 2004; Puig-Gironès *et al.* 2018), and plays an important role as a prey item and as a seed dispersal agent (and thus in plant regeneration). Changes in feeding behaviour may decrease rodent exposure to the negative effects of the presence of predators. Mice that experienced predation pressure demonstrated improved seed movement abilities compared with mice without predator exposure, because

they were capable of moving seeds over longer distances and with greater effort (Leaver and Daly 2003; Feldman *et al.* 2019). The results suggest a causal relationship between foraging activity rates by rodents, stone marten occurrence, and habitat complexity. Therefore, rodents play a crucial role in ecosystems as both prey and seed dispersers, being an indicator of microhabitat complexity and landscape diversity in burnt areas after fires (Stein *et al.* 2014; Kelly and Brotons 2017). This complexity will benefit plant regeneration by rodents and thus make a positive contribution to biodiversity in burnt habitats.

Conclusions

The effects of stone marten and red fox occurrence in the short term on Mediterranean rodent foraging activity can be summarised as follows:

- The responses of predators and prey to wildfires are influenced by the way fire simplifies habitat structure, resulting in an increase in the predation risk.
- Habitat complexity and interspecific competition increase rodent foraging activity rates.
- Stone marten and rodents share similar habitat preferences, which means that the predator signs and the perception of predation risk contribute to the rodent foraging activity rates.
- Red fox occurrence does not affect rodent foraging activity rates.
- In places with high herb cover or no plant cover, acorn removal is lower than in places dominated by shrubs.
- The proximity to rocky outcrops is related to greater stone marten occurrence and higher rodent foraging activity rates.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The datasets analysed during the current study are available in the figshare repository: https://figshare.com/articles/dataset/Stone_marten_modifies_small-rodent_foraging_activity_rates_after_wildfire-Dataset/15168078. doi: 10.6084/m9.figshare.15168078.

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Author affiliations

^ADepartament de Ciències Ambientals, University of Girona, C/Maria Aurèlia Capmany 69, 17003 Girona, Catalonia, Spain.

^BEquip 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, 08028 Barcelona, Catalonia, Spain.