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Original article

Small mammal abundance in Mediterranean post-fire habitats: a role for predators?

I. Torre ^{a,*}, M. Díaz ^b

^a Museu de Granollers-Ciències Naturals, Francesc Macià 51, 08400 Granollers (Barcelona), Spain ^b Departamento de Ciencias Ambientales, Facultad de Ciencias del Medio Ambiente, Universidad de Castilla-La Mancha, 45071 Toledo, Spain

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Abstract

We studied patterns of small mammal abundance and species richness in post-fire habitats by sampling 33 plots (225 m² each) representing different stages of vegetation recovery after fire. Small mammal abundance was estimated by live trapping during early spring 1999 and vegetation structure was sampled by visual estimation at the same plots. Recently–burnt areas were characterised by shrubby and herbaceous vegetation with low structural variability, and unburnt areas were characterised by well developed forest cover with high structural complexity. Small mammal abundance and species richness decreased with time elapsed since the last fire (from 5 to at least 50 years), and these differences were associated to the decreasing cover of short shrubs as the post-fire succession of plant communities advanced. However, relationships between vegetation structure and small mammals differed among areas burned in different times, with weak or negative relationship in recently burnt areas and positive and stronger relationship in unburnt areas. Furthermore, the abundance of small mammals was larger than expected from vegetation structure in plots burned recently whereas the contrary pattern was found in unburned areas. We hypothesised that the pattern observed could be related to the responses of small mammal predators to changes in vegetation and landscape structure promoted by fire. Fire-related fragmentation could have promoted the isolation of forest predators (owls and carnivores) in unburned forest patches, a fact that could have produced a higher predation pressure for small mammals. Conversely, small mammal populations would have been enhanced in early post-fire stages by lower predator numbers combined with better predator protection in areas covered by resprouting woody vegetation.

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1. Introduction

Wildfires are essential components of the dynamics of Mediterranean-type ecosystems (Moreno and Oechel, 1994). Small mammal responses to fire have been extensively studied during the last decades in these ecosystems (see Quinn, 1994; Sutherland and Dickman, 1999, for reviews). In general, small mammal communities recover rapidly after fire following a definite sequence of local colonisations and extinctions of different species that matches closely successional changes in vegetation structure (Prodon et al., 1987; Fox, 1982; Fons et al., 1988; Haim and Izhaki, 1994, 2000). These temporal patterns of change tend to occur even in the absence of some of the usually involved species, a fact that suggests species-specific fire-adapted strategies rather than temporal changes in competitive interactions (Fox, 1982;

Sutherland and Dickman, 1999). The abundance and species richness of small mammals that a given habitat can maintain depends on microhabitat features which provide food and shelter against predators (see Lin and Batzli, 2001 and references therein). Early successional post-fire habitats are covered by herbaceous vegetation, and are accordingly dominated by one or a few species of ground-foraging herbivorous and/or granivorous small mammals (Haim and Izhaki, 1994, 2000). As the cover of woody plants increases and the cover of herbs decreases, these ground-foraging species tend to be replaced by species that feed upon invertebrates and seeds of trees and shrubs under or within woody plants (Prodon et al., 1987; Fons et al., 1988, 1996; Arrizabalaga et al., 1993; Haim et al., 1997).

Small mammals in many communities show preference for habitats with high amount of vegetation cover (Kotler and Brown, 1988), a fact that is closely related with perceived predation risk (Bowers, 1988; Díaz, 1992; Lagos et al., 1995). The selection of dense and thick vegetation is consid-

^{*} Corresponding author.

E-mail address: itorre@teleline.es (I. Torre).

ered to be an antipredatory strategy against both aerial (Longland and Price, 1991) and terrestrial (Jedrzejewska and Jedrzejewski, 1990) predators. However, small mammal mortality due to predation also depends on the local abundance and identity of predators, that can also affect prey reproduction and population dynamics (e.g. Lin and Batzli, 1995; Mappes and Ylönen, 1997; see Hanski et al., 2001, for a review). Predator abundance is also affected by vegetation structure, albeit at larger spatial scales. In the Iberian Peninsula, most small mammal predators are associated with habitats containing well developed woody vegetation (see reviews by Díaz et al. (1996) for diurnal and nocturnal raptors and Blanco (1998) for carnivores). The distribution and abundance of such predators are known to be negatively affected by forest fragmentation due to agricultural expansion (Santos and Tellería, 1998). Although no studies have addressed the successional changes experienced by predator communities after fire, reduced predation pressure in early successional stages and slow recovery is expected as wildfires fragment forest habitats in a very similar way to agricultural expansion (Forman, 1995). Fires can thus increase perceived predation risk for small mammals by reducing the cover of woody plants, at least during the first years after fire (Sutherland and Dickman, 1999), but simultaneously reduce predation pressure by reduction and fragmentation of forest habitats. As the post-fire succession advances, perceived predation risk would decrease due to the recovery of shrub cover and then increase due to the substitution of shrublands by forests with an open understorey, whereas predator abundance and hence predation pressure would increase steadily along the post-fire plant succession from shrublands to forests.

In this paper, we address whether differences in perceived predation risk and predation pressure, related to successional changes in vegetation structure after wildfires, would influence the spatial and temporal patterns of abundance of small mammals. Following a synchronic sampling design, which compares simultaneous measures of small mammal abundance and vegetation structure among plots whose date of last burning is known, we will address (1) how vegetation structure and small mammal communities changed after wildfires and (2) whether the associations of small mammals with antipredatory cover vary with time elapsed since last burning. We expected increased abundances of small mammals as shrub cover increased along the post-fire succession, as well as changes in the strength of these associations in relation to predation pressure. Weaker associations are expected in the low-predator, early successional stages and stronger associations in the high-predator, late successional stages.

2. Study area and methods

Field work was carried out in the Garraf Natural Park (1°52′E, 41°17′N; Barcelona province, NE Spain) in early spring 1999. Fires are recurrent in the area (9 fires/year), although most are small (44.7 ha burnt per fire on average;

Riera, 1996). However, two large fires occurred in 1982 and 1994, that burned 10,000 and 4300 ha, respectively (Riera and Castell, 1997). The natural vegetation of the Park consists of coastal maquis of *Quercus coccifera* and *Chamaerops humilis* and coastal holm oak forests (*Viburno-Quercetum ilicis*), which are dominated by fire-adapted plant species (resprouters after fire, such as *Quercus coccifera*, *Q. ilex, Arbutus unedo, Pistacia lentiscus* or *Erica arborea*, or those with enhanced post-fire germination after fire, such as *Pinus halepensis* and *Cistus* spp.; Naveh, 1974). Due to fire recurrency, most current plant communities in the study area are in a transitional stage, as indicated by the widespread presence of shrublands in relation to forests (65.2% and 11.8% of the surface of the Natural Park surface, respectively; Riera, 1996).

We selected 33 plots according to the time elapsed since their last burning. Nine plots were in areas burnt during the large fire of 1994, another 15 were in areas burnt during the large fire of 1982, but not afterwards, and nine were located in areas that had not been burned at least during the last 50 years (Riera, 1996). Recently-burnt areas are dominated by the herbs Ampelodesmus mauritanica and Brachypodium retusum (ca. 40% cover) with some scattered Quercus coccifera and Pistacia lentiscus shrubs. Mid-successional areas are dominated by either Arbutus unedo and E. arborea shrubs or by young pines *Pinus halepensis* with an understorey dominated by Quercus coccifera and Pistacia lentiscus, whereas the unburned vegetation consists of mature pineoak woodlands. We selected areas burnt in the large forest fires and large unburned areas because their large size allows the location of study plots far from edges, thus avoiding edge effects between habitats with different vegetation structure and, presumably, different communities of small mammal predators (see Murcia, 1995, for a review). All plots were located >80 m from the nearest edge (see García et al., 1998, for a similar approach).

Plots consisted of eight Sherman traps arranged in pairs spaced about 5 m apart to avoid trap saturation, and pairs were located every 15 m along 45 m straight line, covering an area of 225 m². Traps were baited with a mixture of tuna, flour, and oil, and were set under the cover of shrubs or dense herbs to conceal them and to provide some thermal insulation. Traps were open during three consecutive nights and checked every morning, so that total trapping effort was 792 traps/night. The small mammals caught were identified to species, marked with a combination of fur clips and released at the point of capture (Gurnell and Flowerdew, 1990). Due to trap availability and man-power limitations, the 33 plots were not sampled simultaneously, but on three sampling bouts of 11 plots each made between mid-March and late April 1999. As small mammal activity is influenced by moonlight (Price et al., 1984) and moonlight levels changed during the sampling period, we sampled simultaneously during each sampling date a random selection of plots located in areas with different vegetation cover and time elapsed since the last fire (see Díaz, 1992, for a similar approach). We used the number of different individuals trapped as an index of the abundance of each small mammal species in each study plot (Slade and Blair, 2000).

The vegetation structure of each plot was characterised by estimating the values of eight variables in 5 m radius circles centered on each pair of traps (Torre and Bosch, 1999; see Bowers and Dooley, 1993, for a similar approach), and then averaging the values obtained across pairs of the same plot. All variables were transformed before analyses to reach normality and homocedasticity (Zar, 1996). The small size of plots precluded direct measurements of predator abundance on them, so that we had to rely on literature data on the patterns of distribution and diet of raptors and carnivores in Mediterranean forests. We also collected the data available on the species composition of small mammal predator communities in the study area, obtained by the staff of the Natural Park.

The effects of time elapsed since the last fire (short, medium and long) on vegetation structure and small mammal abundances were tested by means of fixed-effects one-way ANOVAs. Small mammal-vegetation structure relationships and its change along the post-fire succession were tested by means of one-way ANCOVAs with time elapsed since the last fire as a fixed factor, small mammal abundances as the dependent variables, and the variables estimating vegetation structure as covariates. To avoid multicolinearlity, we used Principal Components Analysis (PCA) to obtain orthogonal components that were interpreted as gradients of vegetation structure. We used Bonferroni corrections to account for the increase in tablewise type I error when carrying out multiple tests (Rice, 1989).

3. Results

The PCA performed with vegetation structure variables yielded two significant components (eigenvalues > 1; Table 1). The first one accounted for 39% of the original variance and was positively related to cover of trees and

Table 1 Results of the PCA performed with eight structural variables measured at the 33 plots. Only the significant components (eigenvalues > 1) and their significant correlations with the original variables are shown (Bonferroni correction applied, new level of significance to reject independence P = 0.0031)

Variables	PC1	PC2
Cover of trees (%)	0.94	_
Cover of shrubs <1.5 m tall (%)	-0.76	
Cover of shrubs >1.5 m tall (%)		0.75
Shrub height (cm)	0.56	0.62
Cover of herbs <1.5 m tall (%)		-0.88
Herb height (cm)		-0.84
Moss cover (%)	0.68	
Tree density (number/ha)	0.87	
Eigenvalue	3.13	2.66
% Variance explained	39	33
Cumulative % variance	39	72

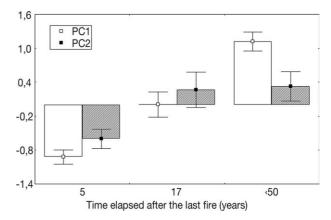


Fig. 1. Mean (±S.E.) values for the two principal components extracted summarising changes in vegetation structure in relation to time elapsed after the last fire. Differences between post-fire levels were significant for PC1 and non-significant for PC2 (see Section 3).

density of logs, the height of shrubs and moss cover, and inversely related to the cover of short shrubs. The second component accounted for 33% of the variance and was an inverse gradient of cover of herbs and a gradient of tall shrubs (>1.5 m). PC1 was considered to represent the changes in vegetation structure related to time elapsed since the last fire, as this component differed significantly among the three post-fire levels (F = 21.00, P < 0.0001; Fig. 1) whereas PC2 did not (F = 2.82, P = 0.07). Recently-burnt areas showed larger covers of short shrubs and herbs, with a low structural variability. The values of variables related to tree categories increased with time elapsed after the last fire, as well as shrub height, the cover of tall shrubs and the cover of mosses, with high structural complexity in the areas not burned in the lasts 50 years or more.

We trapped 120 small mammals (15.15% trapping success). Most of them were wood mice Apodemus sylvaticus (76.1%), followed by white-toothed shrews Crocidura russula (19.2%) and Algerian mice Mus spretus (9.2%). The abundance of small mammals decreased between 17 and 50 years after the last fire (Table 2), a fact that was due to the decreasing trends of the two dominant species. Algerian mice were slightly more abundant in mid-successional stages and were absent from unburned woodlands, although these differences were not significant. Differences in the abundance of small mammals and species richness according to time elapsed after the last fire were related to changes in vegetation structure (Table 3). Significant effects of PC1 were detected for species richness, total abundance, and abundance of C. russula, and marginal effects for the abundance of Apodemus sylvaticus and Mus spretus. PC2 (gradient) did not show significant effects on small mammal abundance and richness. Time elapsed after the last fire affected Apodemus sylvaticus and the total abundance after removing the influence of vegetation structure. In recently burnt plots, (60 months after the last fire) the abundance of wood mice and the overall abundance of small mammals were larger than expected in relation to vegetation traits, and in unburnt areas the observed abundance was smaller than the abun-

Table 2
Mean (±S.E.) values of small mammal abundance and richness in relation to time elapsed after the last fire in the 33 plots sampled. The differences were tested by means of one-way ANCOVA. F and P values are shown

Small mammal abundance	Five years after fire	Seventeen years after fire	Unburned > 50 years	ANOVA F and P
	$(\text{mean} \pm \text{S.E.}) n = 9$	$(\text{mean} \pm \text{S.E.}) n = 15$	$(\text{mean} \pm \text{S.E.}) n = 9$	(n = 33)
Apodemus sylvaticus	3.22 ± 0.49	3.13 ± 0.37	0.55 ± 0.24	15.47, 0.00002
Mus spretus	0.22 ± 0.14	0.60 ± 0.28	0.0 ± 0.0	1.66, 0.20
C. russula	0.89 ± 0.26	0.80 ± 0.32	0.22 ± 0.14	1.44, 0.25
Total	4.33 ± 0.60	4.46 ± 0.71	0.78 ± 0.32	14.61, 0.00003
Richness	1.77 ± 0.14	1.66 ± 0.15	0.66 ± 0.22	8.51, 0.001

Table 3
Results of the one-way ANCOVA analyses of small mammal abundance and richness on time elapsed after the last fire in sampling plots, after controlling for vegetation structure differences between treatments. The effects of time elapsed after fire and the interactions with covariates are expressed as F values, and the effects of each covariate as beta coefficients. Levels of significance are also shown

Effect	Apodemus sylvaticus	Mus spretus	C. russula	Total	Richness
Time elapsed after the last fire	4.92, 0.01	2.43, 0.10	0.64, 0.53	5.60, 0.008	2.26, 0.12
PC1	-0.37, 0.07	-0.39, 0.06	-0.49, 0.01	-0.61, 0.002	-0.53, 0.009
PC2	-0.05, 0.80	-0.28, 0.17	-0.14, 0.45	-0.17, 0.32	-0.19, 0.32
Time after fire PC1	1.40, 0.26	3.70, 0.03	0.71, 0.49	4.84, 0.01	7.03, 0.001
Time after fire \times PC2	0.23, 0.79	0.02, 0.97	0.05, 0.94	0.20, 0.81	0.14, 0.86

dance expected according to the vegetation characteristics of woodlands (Fig. 2). Significant interactions of PC1 with the main effect for the species richness and the total abundance, and marginal interactions for $Mus\ spretus\ (P=0.03)$, revealed that small mammals displayed different microhabitatabundance relationships within areas of different time elapsed since the last fire (Fig. 3). In recently burnt areas (5 years after the last fire) small mammal abundance showed a decreasing trend from dense to scattered shrubland, whereas in unburnt areas or in areas burnt 17 years ago, small mammal abundance was positively associated to the cover of short shrubs.

4. Discussion

Spatial heterogeneity has been described as a major causal factor affecting many biological and ecological processes

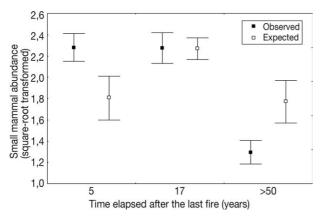


Fig. 2. Observed mean abundances (±S.E.) of small mammals (number of individuals caught in eight traps for each plot) in relation to time elapsed after the last fire, and expected values after controlling for differences in vegetation structure between post-fire levels (one-way ANCOVA adjusted means).

(Wiens et al., 1993; Bowers and Matter, 1997). Landscapes affected by wildfires present a high degree of spatial heterogeneity since wildfires reduce forests to a remnant of forest patches surrounded by a burnt shrubby matrix (Forman, 1995). The spatial distribution, abundance and species composition of small mammal communities in heterogeneous landscapes created by wildfires can be attributed to changes in food availability and shelter as plant succession advances (Quinn, 1994). Furthermore, spatial changes in abundance depend on spatial use relative to axes of habitat heterogeneity (Addicot et al., 1987). Our results confirmed that small mammal abundance and richness decreased through a gradient of increased structural complexity following secondary succession (Haim et al., 1996). This pattern can be attributed to the significant change of cover of short shrubs throughout secondary succession, with higher values in recently burnt areas and lower values in unburnt areas (forests).

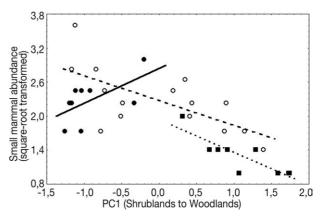


Fig. 3. Relationships between small mammal abundance and the structural gradient represented by the PC1 at plots differing in time elapsed after the last fire (solid line and closed circles, 5 years after fire; dashed line and open circles, 17 years after fire; dotted line and closed squares, 50 years after fire; the interaction was significant at P = 0.01).

Post-fire habitats at early successional stages produced large quantities of seeds and seedlings (Ne'eman et al., 1993), and this could also explain the higher abundance of herbivorous and granivorous species during this period (genus Mus, Haim and Izhaki, 1994, 2000). Otherwise, at early successional stages (1–2 years after fire) the reduced vegetation cover can increase predation risk (Sutherland and Dickman, 1999), but this effect should be reduced by a decrease in predation pressure due to the slow recovery of predator communities after fire as a result of habitat loss and fragmentation (Santos and Tellería, 1998). Predation risk can be even more reduced when the recovery of the small mammal community is completed (6–7 years after fire, Alberton, 1996; Fons et al., 1988), in association with the resprouting of woody vegetation. Conversely, predation risk and predation pressure may increase as the cover of small shrubs decreases and forest cover increases following secondary succession. Forest specialist predators of nocturnal activity tend to be restricted to areas with a well developed tree cover (i.e. tawny owls Strix aluco, Redpath, 1995; common genets Genetta genetta, Ruiz-Olmo and López-Martín, 1995; stone martens Martes foina, Virgós and Casanovas, 1998). Preliminary data on the distribution of small mammal predators in the study area, obtained from the staff of the Natural Park, were in accordance with this general pattern. Only three species have been reported for either short or tall shrublands (red foxes Vulpes vulpes, weasels Mustela nivalis and eagle owls Bubo bubo in short shrubs, and stone marten Martes foina, red foxes and weasels in tall shrubs), whereas forests are occupied by five species (stone martens, red foxes, weasels, common genets and tawny owls). Moreover, photographic records from 101 independent sampling points conducted during six consecutive nights throughout the year 2000, showed that both common genets and stone martens prefer forests against shrublands (genet: 12 presences in forest points and 1 presence in shrubland; stone marten: 10 and 3; absence of both species: 21 and 58, respectively; Peris and Tena, 2000). Predation pressure on small mammals in forest areas would also be higher, than in post-fire stages due to the diet specialisation of forest specialist predators. Most (>90%) preys of genets are small mammals, at least in northern Spain (see Torre et al., 2003 and references therein), and small mammals represented more than half of the prey taken by tawny owls in Spain (Villarán and Medina, 1983).

According to these evidences, early successional stages would be favourable habitats to small mammals due to a combination of reduced predation risk (high vegetation cover) and reduced predation pressure (less predators), and unburnt areas would be unfavourable habitats due to a combination of increased predation risk (low vegetation cover) and increased predation pressure (more predators). Our results are in accordance with this idea, since early successional stages supported larger small mammal abundances than unburnt forests after controlling for structural differences between habitats. In spite of data limitations, these results would also suggest that fire-related forest fragments

could hold lower small mammal abundances than the surrounding shrubby matrix, a pattern that is opposite to that found in forest fragments surrounded by a cropland matrix, where small mammals tend to concentrate in forest edges and small forest fragments (Tellería et al., 1991; Alonso et al., 1996; García et al., 1998; De Alba et al., 2001). Behavioural responses of small mammals to predation (Bowers and Dooley, 1993; Lagos et al., 1995) were also surmised, with positive associations to vegetation cover in unburnt forests and negative associations in early burned habitats. These changes in small mammal-microhabitat relationships suggest differences in perceived predation risk that may have promoted the observed changes in microhabitat use (Sutherland and Dickman, 1999; Lagos et al., 1995).

Our results indicate a possible role of both predation risk and predation pressure on the build-up of small mammal communities along post-fire successions. This hypothesis could also account for other well-established patterns of change of small mammal communities after fire that have been usually explained mainly in terms of responses to changes in vegetation structure, such as the decreasing trend of small mammal diversity through secondary succession (Haim et al., 1996). It should be borne in mind, however, that our conclusions are based on indirect evidences of the responses of either small mammals or their predators to firerelated changes in vegetation structure at the spatial scales relevant to each group. Hence, direct evidence, that must combine both spatial scales (microhabitat and landscape), is needed to ascertain the role of predation in shaping small mammal responses to the post-fire succession in Mediterranean habitats.

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