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Small mammal (Soricomorpha and Rodentia) dynamics after a wildfire in a Mediterranean ecosystem

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Abstract

Small-mammal dynamics after a wildfire were analysed in Serra Calderona Natural Park (Valencian Community, Spain) over a 11-year period. Burned and unburned sites were surveyed seasonally and the trapping success for *Apodemus sylvaticus*, *Mus spretus* and *Crocidura russula* was analysed. Trapping success in both areas, burned and unburned, is influenced by certain climatic variables, namely minimum, average and maximum temperatures, precipitation and relative humidity. Moreover, in the case of *A. sylvaticus*, the most captured species along the entire study period, the influence on capture success of each type of site and the capture period were analysed. Twelve years after the wildfire, both areas presented the same qualitative and quantitative small-mammal composition. However, trapping success for *A. sylvaticus* was greater at the burned sites in 6 out of 11 study years, although with similar annual fluctuations in the two areas. The effect of the considered climatic variables on small-mammal species populations seems to be stronger in the burned area than in the unburned area, which is probably due primarily to the regeneration process after a wildfire.

Keywords: Mediterranean ecosystems; population dynamics; post-fire regeneration; Serra Calderona; small mammals.

Introduction

Wildfires exert a great perturbation capacity in the ecosystems and in the history of life on Earth (Bowman et al. 2009, Pausas and Keeley 2009). Consequently, studying their effects as well as the related post-fire regeneration process of the affected ecosystems is of vital importance. When a wildfire takes place, many effects and repercussions directly or indirectly affect every geological and biological layer; soil, vegetation and fauna. Severe alterations in the succession and organisation of vegetational communities take place, modifying the physical conditions of the environment and provoking changes in the presence, distribution and density of certain species (Bowman et al. 2009). As with vegetation, fires affect animals both directly and indirectly. Their response to a wildfire is complex, reflecting the varying food and shelter requirements of some species, their exposure to predation, and other factors (Letnic et al. 2005). After a fire, the vegetational and animal regeneration of the affected ecosystem start simultaneously in a highly variable manner depending on numerous external factors, such as edaphology, climate and vegetation (Fons et al. 1988, Fuentes et al. 2000, Torre and Díaz 2004).

Numerous studies have analysed the impact of wildfires on soil, vegetation, birds, invertebrates as well as small mammals in Mediterranean ecosystems in France (Prodon et al. 1984, 1987, Athias-Binche et al. 1987; Fons et al. 1988, 1993), Spain (Arrizabalaga et al. 1993, Fuentes and Galán-Puchades 1994, Arrizabalaga and Llimona 1996, Torre and Díaz 2004, Torre et al. 2005, Pons 2007, Santos et al. 2009), Israel (Haim 1993, Broza and Izhaki 1997) and Australia (Fox 1982, 1990, Fox et al. 2003, Letnic and Dickman 2005, Letnic et al. 2005) as well as in other types of ecosystems (e.g., Clark and Kaufman 1990, Brown et al. 1998, Vieira 1999, Fisher and Wilkinson 2005, Zwolak and Foresman 2007).

According to Bombí et al. (2002), small mammals (Soricomorpha and Rodentia) may be considered valuable indicators (biological tags) of changes in the productivity of an ecosystem as their response correlates with the degree of alteration and/or recuperation of forests. Their distribution and abundance are basically conditioned by the structure of their habitat and vegetational succession stands out as the main cause of the changes associated with the small-mammal community structure (MacMahon 1981, Meserve et al. 1995, Arrizabalaga and Llimona 1996, Monamy and Fox 2000). Soricomorphs and rodents depend on the availability of suitable microhabitats for protection, nesting and food supply, which, in turn, depend on the supportive capacity of the habitat. Consequently, forest fires may exert a strong influence on the structure and functioning of small-mammal communities (Zwolak and Foresman 2007). Also, small mammals play a vital part in the succession of any perturbed Mediterranean environment. They are the main source of food of many forest predators (thus representing a link between primary producers and secondary consumers), and they intervene in the process of seed dispersion and forest regeneration itself (Ordóñez and Retana 2004). For all these reasons, small mammals are a fundamental tool in the post-fire regeneration process since they reflect the gradual recuperation of invertebrates (in the case of insectivores), changes in vegetation (determining food availability and potential shelter), soil conditions (affecting the development of the vegetation) and climatic conditions which directly or indirectly affect their behaviour. Hence, the study of soricomorphs and rodents is, primarily, a direct analysis of

fauna regeneration and, secondarily, an indirect analysis of the regeneration conditions of the affected ecosystem.

The influence of climate on small-mammal population dynamics in disturbed areas has rarely been studied, in contrast to, for example, vegetation structure. However, as anticipated, the dynamics of each small-mammal species is influenced by climate variations, such as thermal and moisture variances, and other abiotic factors in the burned area, especially within the first years after the wildfire. In contrast, these effects are less important in the unburned sites, because they are buffered by existent vegetation structure against fluctuations in climate. To confirm this hypothesis, the present study analyses small-mammal dynamics along the post-fire period at burned and unburned sites of the same Mediterranean area.

Materials and methods

Study area

The study area, Serra Calderona Natural Park, is a Spanish Mediterranean ecosystem located between the provinces of Castelló and València, Valencian Community (39°35′–39°51′N, 0°15′–0°43′W) (Figure 1). This mountain range, with a total surface of approximately 52,000 ha, suffered a devastating wildfire at the end of the summer of 1992 affecting a total of 9500 ha including forests and cultivated land which had been left untended.

The climate is typically Mediterranean, with irregular rainfall and intense summer droughts. The eastern and meridional regions correspond to the thermomediterranean bioclimatic setting with a dry ombroclimate. In contrast, the westernmost and septentrional regions are included in the mesomediterranean bioclimate, with a little more rainfall but not fully qualifying as a subhumid ombroclimate (Perez-Cueva 1994). Chorologically, the vegetation corresponds to the western Mediterranean sub-region (Costa 1986, Garcia-Fayos 1991). As a consequence of the continuous degradation due to anthroponisation (cultivation, charcoal production, grazing and building activities) and numerous wildfires, potential vegetation is largely restricted to various substitution stages, principally littoral kermes oak (*Quercus cocciferae-Pistacietum lentisci*) and continental kermes oak (*Rhamno lycioidis-Quercetum cocciferae*), along with different types of shrubs and pastures.

Zoological data

A multidisciplinary project on the post-fire dynamics of small mammals was initiated in February 1994, the winter of the 2nd post-fire year (PFY), and continued until 2004, the 12th PFY.

A trapping protocol was established to elucidate and compare the community dynamics and structures of small mammals within and between burned and unburned sites. A comprehensive description of the trapping method and study procedures was previously provided by Fuentes et al. (1998, 2000) and Galán-Puchades et al. (1999). This method is based on the square plot (quadrate) technique, on a seasonal basis, i.e., four times annually at intervals of 3 months, and depending on soil and climatic conditions. Fifty-five hand-made wire-mesh traps (sized 23×10×10 cm; using bread dipped in olive oil as bait) were placed at night within a distance of 10–15 m forming a square at each population study site, and the capture-release method was applied. Trapping took place on three consecutive days, traps were checked approximately every 24 h, and to minimise weather influence on the trapping success, trapping sessions were postponed on days with heavy rainfall or extreme temperatures. The captured animals were identified at species level and weighed, sexual activity was determined, they were marked with a lasting colourant on different parts of the abdomen and/or the thorax, and released at the place of capture.

Three trapping sites were set up in the study area: two in the burned area and one in the unburned area. The latter site presented similar ecological conditions as the burned sites before the fire and is situated in a straight line about 6 km away from them to minimise nearness effects resulting from the mobility of the small mammals. The two burned sites were considered as one, as both biotopes are very close and have a great ecological similarity, and their data were pooled.

Climate and vegetation data

Data on daily maximum, minimum and mean temperatures in °C, mean monthly precipitation in mm, number of rainy days,

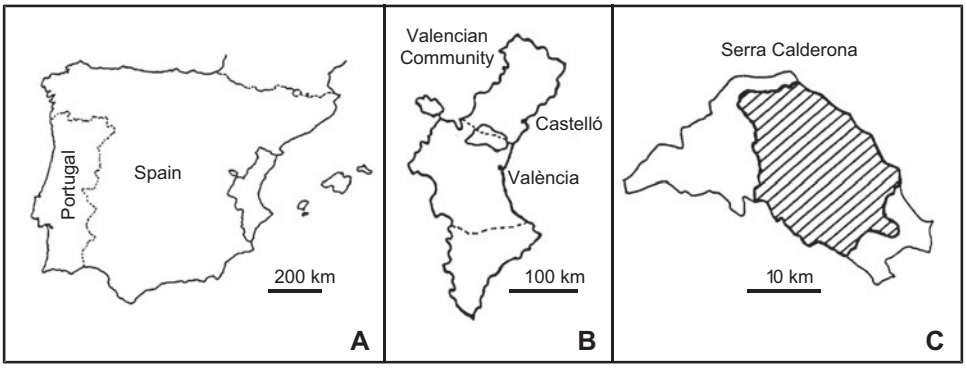

Figure 1 Geographical setting of the study area in the (A) Iberian Peninsula, (B) in the Valencian Community and in (C) Serra Calderona.

monthly relative humidity values in%, as well as monthly total evaporation in mm, were compiled from three meteorological stations of the Agencia Estatal de Meteorología situated within Serra Calderona.

Vegetational recovery in the burned area was gradual and steady after the 2nd and 3rd PFY, when Mediterranean shrubs reappeared and substituted primary succession plants, especially grass (Gramineae). Successively, the land was re-covered by shrubs, reaching an average height of 60 cm between the 11th and 12th PFYs, while pine trees (the Alepo pine, *Pinus halepensis*, and the maritime pine, *P. pinaster*) reappeared, reaching ca. 1.5 m at the end of the current study period. However, only vegetational changes related to changing seasons are noteworthy in the unburned area during the study period. Instead of a vegetation recovery index, annual NDVI (normalised difference vegetation index) data from the burned and the unburned sites were considered in the analysis as an independent variable. This index shows the general response of vegetation to rainfall, with values ranging from -1.0 to 1.0, where increasing positive values indicate increasing green vegetation and lesser values indicate non-vegetated surface features (Eidenshink and Faundeen 1997). The data were obtained at a resolution of 1 km from AVHRR images of the TIROS-NOAA satellite, following the methodology described by Fuentes et al. (2007). Climate and NDVI data compiled since 1991 (1 year before the wildfire) until Oct 2002 (10th PFY) were integrated into a multidisciplinary database, also including zoological data and other thematic layers.

Analysis of small-mammal dynamics

Species-specific trapping success, climatic and NDVI variables, site and period of capture were evaluated to analyse and compare small-mammal dynamics at the burned and unburned sites. The number of individuals captured per 100 trap-nights at each site, year and season were analysed together with the relative abundance of each species (different individuals of each species captured/total number of individuals captured) at each site to determine possible differences along the post-fire regeneration process by means of the χ^2 or Pearson's test (Parker 1981). Moreover, linear trend, χ^2_t, and χ^2 for departure from linear trend, $\chi^2_d=\chi^2-\chi^2_t$, among the annual trapping success were calculated (Zar 2010).

To estimate the possible influence of climate and the vegetation recovery on the small mammals captured at the studied sites, simple and multiple linear regressions were carried out, using the stepwise method for multiple regressions (which includes or eliminates independent variables successively until the best model has been obtained). NDVI and climatic variables corresponding to the year of capture, as well as those of the previous year, were used as independent variables, and the annual number of individuals of each small-mammal species captured per 100 trap-nights, transformed using arc-sin (Zar 2010), was used as the dependent variable. Moreover, in the case of *Apodemus sylvaticus* (Linnaeus, 1758), the precipitation values corresponding to the period of April to October (spring/summer period) of the year of capture as well as those prior to the year of capture were also used as independent variables.

The influence exercised by site type (burned or unburned) and capture period on the number of individuals captured per 100 trap-nights of *Apodemus sylvaticus* was also analysed, using a 2- and 3-way ANOVA. Capture period refers to the seasonal period (autumn/winter or spring/summer) of each PFY. To establish which factors are a source of variation, and if these are determined by the post-fire regeneration process, the number of individuals captured per 100 trap-nights was analysed on a global level (considering captures at the burned and the unburned sites together) as well as separately.

Stat View 5.0 (SAS Institute Inc., Cary, NC, USA) and SPSS 15.0 (SPSS Inc., Chicago, IL, USA) for Windows were used for statistical procedures, statistical significance was established at $p<0.05$, co-linearity of the independent variables was examined and assumptions of normality, linearity, homoscedasticity and independence assessed.

Results

Small-mammal population dynamics

During the entire 11-year study period, 1830 small mammals (10.84% trapping success) of four species were captured: the wood mouse, *Apodemus sylvaticus*, the Mediterranean mouse, *Mus spretus* (Lataste, 1883), the greater white-toothed shrew, *Crocidura russula* (Hermann, 1780), and the black rat, *Rattus rattus* (Linnaeus, 1758). The most captured species was *A. sylvaticus* (n=1552; 9.19 individuals per 100 trap-nights), followed by *M. spretus* (n=137; 0.81 individuals per 100 trap-nights) and *C. russula* (n=130; 0.77 individuals per 100 trap-nights), while *R. rattus* was the species with the lowest trapping success (n=11; 0.07 individuals per 100 trap-nights).

At the burned sites, 1399 small mammals (12.38 individuals per 100 trap-nights) were captured. *Apodemus sylvaticus* (n=1213; 10.73 individuals per 100 trap-nights) was the species with the highest capture percentage, followed by *Mus spretus* (n=96; 0.86 individuals per 100 trap-nights) and *Crocidura russula* (n=80; 0.71 individuals per 100 trap-nights).

At the unburned site, 431 small mammals (7.73 individuals per 100 trap-nights) were captured. Similar to the burned sites, *Apodemus sylvaticus* was the dominant species (n=339; 6.08 individuals per 100 trap-nights), followed by *Crocidura russula* (n=50; 0.90 individuals per 100 trap-nights) and *Mus spretus* (n=41; 0.73 individuals per 100 trap-nights).

The trapping success for *Rattus rattus* was negligible at either site and is therefore not included in the study.

In general, trap mortality, always below 10%, was similar in both areas, although it was slightly greater at the burned sites in the first years.

Apodemus sylvaticus The χ^2 analysis for the annual trapping success showed significant statistical differences between PFYs at burned ($\chi^2_{[10]}=713.137$; $p<0.0001$) and unburned ($\chi^2_{[10]}=309.448$; $p<0.0001$) sites, while the test for linear trend showed that there was no linear trend among the annual trapping success at burned ($\chi^2_{d\ [9]}=294.014$;

p<0.0001) and unburned ($\chi^2_{d\ [9]}$=153.504; p<0.0001) sites. However, when comparing each year with the previous one, the significant increase of the trapping success during various years in both areas stands out (Table 1). In the annual pairwise comparison between both areas, the dynamics of the annual trapping success for the wood mouse over time (Figure 2) were very similar. Nevertheless, the trapping success for this species at the burned sites was greater in each study year, except for the 3rd PFY, in which the trapping success was higher at the unburned site. Statistically significant differences were detected in 6 PFYs (Table 2).

Mus spretus At the burned sites, not only the non-detection of *M. spretus* until the 3rd PFY is remarkable, but also the increase of its trapping success during the 5th PFY ($\chi^2_{[1]}$=4.174; p=0.0410) and the 6th PFY ($\chi^2_{[1]}$=11.012; p=0.0009) as well as its non-detection in the 8th and the 9th PFY. However, it remained undetected at the unburned site in 6 of the 11 study years, i.e., from the 3rd to the 5th, and the 7th to the 9th PFY (Figure 3).

Crocidura russula At the burned sites, the detection of *C. russula* during the first study year (2nd PFY) was rather unusual. This soricomorph experienced an increase in the 5th PFY ($\chi^2_{[1]}$=14.618; p<0.0001), but remained undetected during the 7th PFY, and its trapping success remained also very low during the next years although slowly and gradually recovering. At the unburned site, its trapping success remained practically unchanged for a great part of the period analysed, although it remained undetected during the 8th and the 9th PFYs. In the first study years, the trapping success for *C. russula* was relatively similar in both areas (Figure 4), but its trapping success was higher at the burned sites during the 5th PFY ($\chi^2_{[1]}$=5.675; p=0.0172). Furthermore, greater trapping success at the unburned site during the 10th PFY ($\chi^2_{[1]}$=9.183; p=0.0024) and the 11th PFY ($\chi^2_{[1]}$=10.859; p=0.0010) was remarkable.

Influence of abiotic factors on the trapping success

Climate and vegetation recovery The analysis of NDVI and climatic variables influencing small mammals in both areas (Tables 3 and 4) shows that accumulated precipitation during the period prior to capture had a positive influence on the three species at the burned sites, but only on *Apodemus sylvaticus* and *Crocidura russula* at the unburned site. Mean and maximum temperature of the previous year exercised a great influence on the trapping success for *A. sylvaticus* at the burned sites only, while relative humidity influenced its trapping success in both areas. *Mus spretus* seemed to be influenced by the interaction of maximum and minimum temperatures at the burned sites only, however, there was no correlation with the variables considered at the unburned site, probably due to the low number of individuals captured.

Site type, PFY and capture period The PFY and the type of site had an important influence on the trapping success for *Apodemus sylvaticus*, as shown by the 3-way ANOVA analysis (Table 5). In contrast, the type of site and the PFY determined the impact of the capture period, which on its own did not seem to have any significant effect.

The aforementioned results are confirmed by the 2-way ANOVA analysis for each type of site (Table 6). At the burned sites, the trapping success for *Apodemus sylvaticus* was influenced by the PFY, the capture period and their interaction, while the only source of variation at the unburned site seem to be the PFY.

Table 1 Statistical differences between annual trapping success for *Apodemus sylvaticus* at burned and unburned sites.

PFYs	Burned sites		Unburned site	
	χ^2	p-value	χ^2	p-value
4th–3rd	159.544	<0.0001	–	–
5th–4th	–	–	8.713	0.0032
6th–5th	–	–	23.256	<0.0001
11th–10th	53.803	<0.0001	45.522	<0.0001
12th–**11th**	24.969	<0.0001	4.418	0.0356

Highest annual trapping success, years in bold. PFY, post-fire year; degrees of freedom, df=1.

Discussion

Limitations resulting from the population estimate have to be considered in the analysis of the results obtained in this study: first, sources of variation in capture probabilities of small mammals between burned and unburned sites in space and time can also be associated with the trapping effort and weather variations; and, second, as suggested by McKelvey and Pearson (2001), the use of a population index instead of a population-estimation model. Moreover, to interpret the influence of climate on the regeneration process, the stronger effects of climate variability on the burned sites, due to re-growing vegetation which still cannot buffer climate fluctuations, have to be considered.

On a global level, *Apodemus sylvaticus* was the predominant species in both areas due to its wide distribution in Mediterranean forests, the wide range of food it consumes (Gosálbez 1987, Torre et al. 2002) and its generalist character (Torre et al. 2001, Reutter et al. 2003), providing it with great flexibility when faced with changes and perturbations of its habitat. Trapping success for *Crocidura russula* and *Mus spretus* was very similar even at the burned sites, although their diets are very distinct (insectivorous vs. granivorous), and *C. russula* is ecologically more demanding (Fuentes et al. 1998). This result may be due to the fact that the two species share a similar microhabitat (Torre and Arrizabalaga 2000). As both species do not compete for food, factors other than food competition are likely to be the cause of their dissimilar population dynamics. The comparative analysis between the burned and unburned sites showed that 12 years after the fire, the two

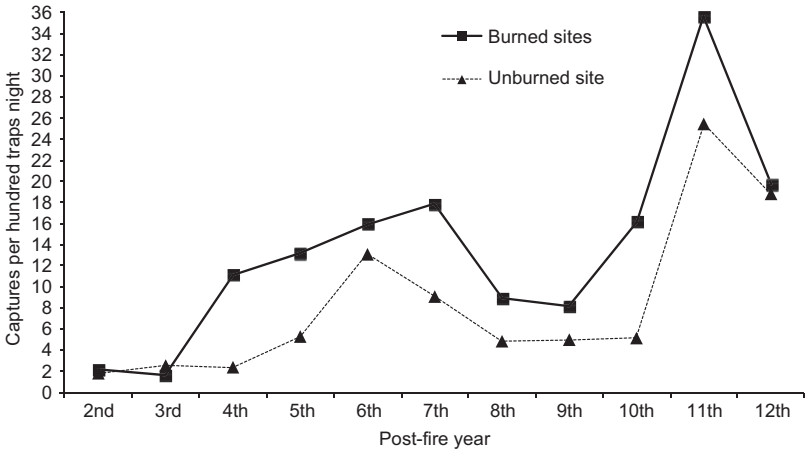

Figure 2 Annual fluctuation of the trapping success (number of individuals captured per 100 trap-nights) for *Apodemus sylvaticus* at the burned sites (uninterrupted line) and at the unburned site (dotted line).

small-mammal communities had reached qualitative and quantitative similarity.

The annual study of the burned sites showed that small-mammal post-fire recuperation is characterised by the dominance of *Apodemus sylvaticus* during the entire study period. Along the years, this species, already recognised as a post-fire colonizer in the regeneration process in Serra Calderona (Fuentes et al. 1998), had an increasing chance of finding shelter and food in the burned area thanks to vegetational re-growth. At the same time, its exposure to potential predators was lower for their succession process is usually much longer. The growth of the wood mouse population may have been related to the aforementioned factors, also reflected by its increased trapping success from the 4th PFY onwards. Moreover, its trapping success was almost always greater at the burned sites, with significant differences in 6 out of 11 study years. According to Torre and Díaz (2004) and Torre et al. (2005), these results seem to be due to the positive association of small mammals with the shrub-like and low herbaceous layers which characterise the burned area's transitory environment of secondary succession together with a reduced predation risk and low predation pressure. However, according to other studies, the causes of small-mammal post-disturbance dynamics may be more complex, including not only factors such as vegetation recovery, climate conditions, food availability, predation risk and predation pressure, but also changes in the reproductive cycle and a decrease in fecundation capacity, which in turn regulate populational growth (Torre and Arrizabalaga 2002, Torre et al. 2002, Reed and Slade 2008).

Table 2 Statistical differences between *Apodemus sylvaticus* annual trapping success at burned and unburned sites.

PFYs	χ^2	p-value
4th	58.906	<0.0001
5th	35.508	<0.0001
7th	12.680	0.0004
8th	4.690	0.0303
10th	23.566	<0.0001
11th	6.559	0.0104

Annual trapping success is always higher at the burned sites. PFY, post-fire year; df=1.

Likewise, the conditions of the burned area seemed to favour *Mus spretus* as reflected by the fact that it was caught in 8 out of 11 study years, while it was detected at the unburned site in only 5 out of 11 years. Although the different frequency of capture between the two types of sites was not statistically significant, the shrub-like development may have favoured *M. spretus*, mainly in the first years of the regeneration process, which is also in agreement with Torre and Díaz (2004), who suggested a greater mean abundance of this species in such areas.

Fons et al. (1988) reported that the reappearance of *Crocidura russula* does not occur until 5 years after the fire, which contrasts with the detection of this soricomorph in the burned area of Serra Calderona from the first study year (2nd PFY) onwards. Moreover, our findings agree with similar results obtained by Arrizabalaga et al. (1993) and Fons et al. (1993) in other Mediterranean areas. The annual trapping success for *C. russula* was similar at the two types of sites, although it was greater at the burned sites during the 5th and 6th PFY. These results are explicable by the persistence of this soricomorph, having found shelter among the remnants of walls of untended fields. Moreover, they also reflect the quick recovery of the burned area's vegetal cover (Fons et al. 1993).

Carrying out a comparative analysis of the annual trapping success for *Apodemus sylvaticus, Mus spretus* and *Crocidura russula* for both areas allows for the distinction between treatment events (taking place only in the burned area) and non-treatment events (taking place simultaneously at both types of sites), e.g., the growth rates of all three species reach their peaks, in burned and unburned sites, after the 10th PFY. This coincidence occurring at the burned and unburned sites suggests that their increase is due to climatic factors, namely accumulated precipitation and relative humidity, which positively influence food availability and thus the increase of

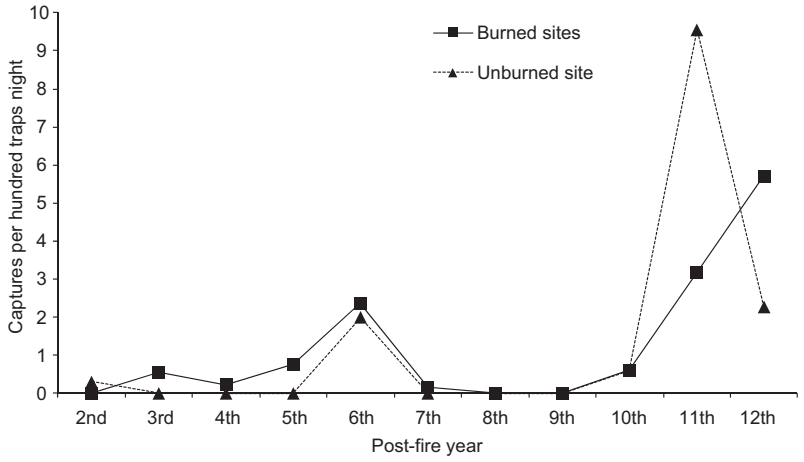

Figure 3 Annual fluctuation of the trapping success (number of individuals captured per 100 trap-nights) for *Mus spretus* at the burned sites (uninterrupted line) and at the unburned site (dotted line).

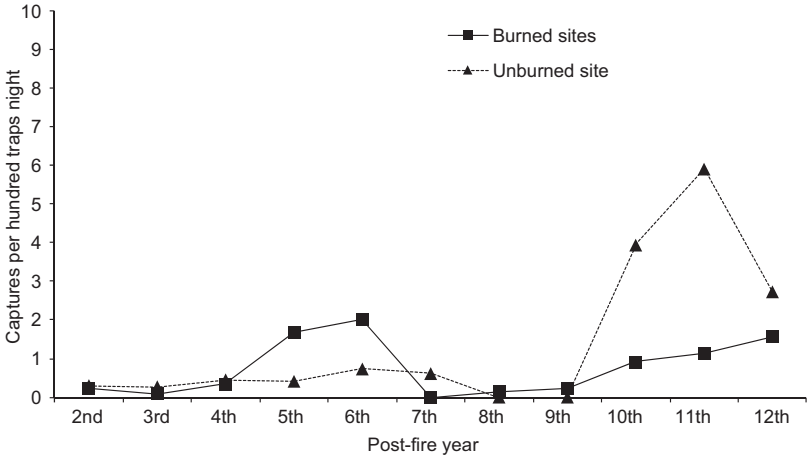

Figure 4 Annual fluctuation of the trapping success (number of individuals captured per 100 trap-nights) for *Crocidura russula* at the burned sites (uninterrupted line) and at the unburned site (dotted line).

Table 3 R^2 values obtained by simple and multiple linear regressions between the annual trapping success (number of individuals captured per 100 trap-nights) at the burned sites, NDVI and climatic variables.

Small-mammal species	Variables	R^2	B_i	*SE*	p-value
Apodemus sylvaticus	Tmean-year before	0.328	-0.088	0.038	0.049
	Tmax	0.425	-0.080	0.030	0.034
	Tmax-year before	0.406	-0.102	0.038	0.028
	PP-year before	0.328	0.001	0.000	0.038
	RH	0.501	0.031	0.010	0.020
Mus spretus	PP-year before	0.495	0.00003	0.000	0.014
	Tmax	0.510	-0.042	0.014	0.019
	Tmax×Tmin	0.722			0.018
	Tmax		-0.064	0.014	0.006
	Tmin		0.061	0.022	0.042
Crocidura russula	PP-year before	0.468	0.00002	0.000	0.029

B_i, partial regression coefficient; Tmean, daily mean temperature (°C); Tmax, daily maximum temperature (°C); Tmin, daily minimum temperature (°C); PP, accumulated precipitation (mm); RH, relative humidity (%).

Table 4 R^2 values obtained by simple and multiple linear regressions between the annual trapping success (number of individuals captured per 100 trap-nights) at the unburned site, NDVI and climatic variables.

Small-mammal species	Variables	R^2	B_i	*SE*	p-value
Apodemus sylvaticus	PP-year before	0.484	0.001	0.000	0.010
	RH-year before	0.498	0.033	0.011	0.014
	RH×Tmin (year before)	0.699			0.011
	RH-year before		0.043	0.010	0.005
	Tmin-year before		0.108	0.043	0.044
	RH×Tmin×PP (year before)	0.918			0.001
	RH-year before		0.032	0.006	0.003
	Tmin-year before		0.121	0.022	0.003
	PP-year before		0.001	0.000	0.009
Crocidura russula	PP-year before	0.472	0.00004	0.000	0.017

B_i, partial regression coefficient; PP, accumulated precipitation (mm); RH, relative humidity (%); Tmin, daily minimum temperature (°C).

population density (Meserve et al. 1995; Torre et al. 1996, 2002, Ernest et al. 2000). This postulation is supported by the strong increase in precipitation during the 9th and the 10th PFY. This result agrees with other authors who also found precipitation to have a positive influence on small-mammal dynamics (Torre et al. 1996, Torre and Arrizabalaga 2002). Furthermore, the increase in precipitation enhances plant productivity in terrestrial ecosystems (Kelt et al. 2004, Squeo et al. 2006), leading to a significant increase in ephemeral cover, soil seed density (Gutiérrez and Meserve 2003, Meserve et al. 2003) and insects (Fuentes and Campusano 1985). On the other hand, heavy rainfall may relax territorial behaviour and competitive social interactions between individuals as increased plant productivity favours an increment of the fraction of breeding individuals (Lima et al. 2001). In fact, according to Torre (2004), after periods of high levels of cumulative rainfall the breeding activity of females, the recruitment of juveniles and the population growth rate are significantly favoured. Although the results obtained show the importance of accumulated precipitation for the three species considered, and also of relative humidity in the case of *A. sylvaticus*, the influence of other climatic factors depends on the species and the type of site. The negative influence of the mean and maximum temperature on the trapping success for *A. sylvaticus*, exercised solely at the burned sites, suggests that features of the affected ecosystem play an important role in the dynamics of this rodent. The lack of correlation between vegetation data, represented by NDVI, and trapping success was surprising, mainly because NDVI shows the response of vegetation to rainfall, but also because in other studies on burned Mediterranean ecosystems with a similar post-fire vegetal evolution (Arrizabalaga and Llimona 1996), such a correlation was found. It is likely that annual NDVI and trapping success data cannot reliably confirm this potential correlation. Thus, future studies analysing the structure of small-mammal populations should also include seasonal data of these and further variables.

Table 5 Influence of site type (burned and unburned), post-fire year (PFY) and capture period on trapping success for *Apodemus sylvaticus* by means of ANOVA.

Source of variability	Trapping success		
	df	*F*	p-value
Site type	1	32.281	0.0001
PFY	10	20.345	0.0001
Site type×Capture period	1	6.581	0.0185
PFY×Capture period	10	7.715	0.0001

The significant effect of an interaction between PFY and capture period on the trapping success for *Apodemus sylvaticus*, at the burned sites only, demonstrates that the regenerative state of the burned area (determined by the PFY) conditions the influence of climatic factors. The higher arboreal development together with the vegetal cover of the unburned site alleviate the effects of seasonal variations, while in the post-fire area, still in regeneration, seasonal variations may have a direct influence on the behaviour of the *A. sylvaticus* population. This influence could be determined by the degree of regeneration (the vegetal cover of the burned area recovers quickly and in agreement with the typical vegetal succession of Mediterranean forests affected by a

Table 6 Influence of the post-fire year (PFY) and capture period on the trapping success for *Apodemus sylvaticus* at each site type (burned and unburned) by means of ANOVA.

Source of variability	Trapping success at the burned sites			Trapping success at the unburned site		
	df	*F*	p-value	df	*F*	p-value
PFY	10	18.358	<0.0001	10	6.410	0.0035
Capture period	1	11.820	0.0064	1	–	–
PFY×Capture period	10	10.278	0.0005	10	–	–

wildfire) as shown by the greater influence that the PFY-factor plays at the burned sites.

Our results suggest that the succession of soricomorphs and rodents can be correlated to vegetal succession after a wildfire, corresponding to the degree of alteration and/or the recuperation of forests. Small-mammal population dynamics can be considered a reliable biological tag of the changes experienced by perturbed Mediterranean ecosystems, a consequence mainly of climate variations, behind, for example, the vegetal regeneration process and food availability, at burned sites.

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References

Arrizabalaga, A. and F. Llimona. 1996. Effect of fire on fauna and the recuperation of fauna after fire. In: (J. Terrades, ed.) Ecologia del Foc. Edicions Proa, Barcelona. pp. 173–188 (in Catalan).

Arrizabalaga, A., E. Montagud and R. Fons. 1993. Post-fire succession in small mammal communities in the Montserrat Massif (Catalonia, Spain). In: (L. Trabaud and R. Prodon, eds.) Fire in Mediterranean Ecosystems. Commission of the European Communities, Brussels. pp. 281–291.

Athias-Binche, F., F. Briard, R. Fons and F. Sommer. 1987. Study of ecological influence of fire on fauna in Mediterranean ecosystems (soil and above ground layer): patterns of post-fire recovery. Ecol. Medit. 13: 135–154.

Bombí, A., C. Castell, D. Guinart, S. Llacuna and A. Miño. 2002. Los planes de seguimiento en los parques naturales gestionados por la Diputación de Barcelona. Ecosistemas 11: 1–12.

Bowman, D.M.J.S., J.K. Balch, P. Artaxo, W.J. Bond, J.M. Carlson, M.A. Cochrane, C.M. D'Antonio, R.S. DeFries, J.C. Doyle, S.P. Harrison, F.H. Johnston, J.E. Keeley, M.A. Krawchuk, C.A. Kull, J.B. Marston, M.A. Moritz, I.C. Prentice, C.I. Roos, A.C. Scott, T.W. Swetnam, G.R. van der Werf and S.J. Pyne. 2009. Fire in the Earth system. Science 234: 481–484.

Brown, K.L., L.S. Gadd, T.W. Norton, J.E. Williams and N.I. Klom. 1998. The effects of fire on the fauna in the Australian Alps National Parks: a database. The Johnstone Centre Report 118. Charles Sturt University, Albury Wodonga, Australia, pp. 50.

Broza, M. and I. Izhaki. 1997. Post-fire arthropod assemblages in Mediterranean forest soils in Israel. Int. J. Wildland Fire 7: 317–325.

Clark, B. and D.W. Kaufman. 1990. Short-term responses of small mammals to experimental fire in tallgrass prairie. Can. J. Zool. 68: 2450–2454.

Costa, M. 1986. La vegetación del País Valenciano. Publicacions Universitat de València, València. pp. 240.

Eidenshink, J.C. and J.L. Faundeen. 1997. Acquiring, archiving, processing, and distributing a 6-Terabyte Global Land Data Set. International Society for Photogrametry in Remote Sensing. In: (D. Rosenholm and H. Osterlund, eds.) ISPRS Joint Workshop, from producer to user. International Society for Photogrammetry and Remote Sensing, Washington, D.C. pp. 52–55.

Ernest, S.K.M., J.H. Brown and R.R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88: 470–482.

Fisher, J.T. and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal. Rev. 35: 51–81.

Fons, R., I. Grabulosa, C. Feliu, S. Mas-Coma, M.T. Galán-Puchades, A.M. Comes. 1993. Postfire dynamics of a small mammal community in a Mediterranean forest (*Quercus suber*). In: (L. Trabaud and R. Prodon, eds.) Fire in Mediterranean Ecosystems. Commission of the European Communities, Brussels. pp. 259–270.

Fons, R., I. Grabulosa, M.C. Saint-Girons, M.T. Galán-Puchades and C. Feliu. 1988. Incendie et cicatrisation des écosystèmes méditerranéens. Dynamique de repeuplement en micromammifères. Vie Milieu 38: 259–280.

Fox, B.J. 1982. Fire and mammalian secondary succession in an Australian coastal heath. Ecology 63: 1332–1341.

Fox, B.J. 1990. Changes in the structure of mammal communities over successional time scales. Oikos 59: 321–329.

Fox, B.J., J.E. Taylor and P.T. Thompson. 2003. Experimental manipulation of habitat structure: a retrogression of the small mammal succession. J. Anim. Ecol. 72: 927–940.

Fuentes, E.R. and C. Campusano. 1985. Pest outbreaks and rainfall in the semi-arid region of Chile. J. Arid Environ. 8: 67–72.

Fuentes, M.V. and M.T. Galán-Puchades. 1994. Small-mammal recolonization in burned areas and their role as biological tags of post-fire regeneration. The case of Serra Calderona: preliminary data. In: Segon Congrés d'Estudis Comarcals. Institut d'Estudis Comarcals del Camp de Túria, Benaguasil, València. pp. 104–113 (in Catalan).

Fuentes, M.V., M.T. Galán-Puchades and A.M. Cerezuela. 1998. Insectívoros y roedores de la Serra Calderona (Comunitat Valenciana). Dinámicas de recolonización y estudio helmintológico postincendio. Galemys 10: 37–58.

Fuentes, M.V., A.M. Cerezuela and M.T. Galán-Puchades. 2000. A helminthological survey of small mammals (insectivores and rodents) in the Serra Calderona mountains (Valencian Community, Spain). Res. Rev. Parasitol. 60: 25–35.

Fuentes, M.V., S. Sainz and M.T. Galán-Puchades. 2007. Geographic information systems as a new tool and methodology proposed for modeling mammal/helminth postfire regeneration. The example of Parc Natural de la Serra Calderona (Comunitat Valenciana, Spain). Res. Rev. Parasitol. 67: 9–14.

Galán-Puchades, M.T., M.V. Fuentes, A. Cerezuela, R. Fons and S. Mas-Coma.1999. A proposed methodology for the use of helminth parasites as biological tags in the study of postfire ecosystem regeneration processes. Vie Milieu 49: 45–50.

Garcia-Fayos, P. 1991. La vegetación silicícola de la Sierra Calderona (Comunidad Valenciana). Lazaroa 12: 317–332.

Gosálbez, J. 1987. Insectivores and rodents from Catalonia. Methodology of study and faunistic catalog. Ketres Editora, Barcelona. pp. 241 (in Catalan).

Gutiérrez, J.R. and R.L. Meserve. 2003. El Niño effects on soil seed bank dynamics in north-central Chile. Oecologia 134: 511–517.

Haim, A. 1993. Resilience to fire of rodents in an east-Mediterranean pine forest on mount Carmel, Israel: the effects of different managements. In: (L. Trabaud and R. Prodon, eds.) Fire in Mediterranean Ecosystems. Commission of the European Communities, Brussels. pp. 303–314.

Kelt, D.A., P.L. Meserve, K. Nabors, M.L. Forister and J.R. Gutiérrez. 2004. Foraging ecology of small mammals in semiarid Chile: the interplay of biotic and abiotic effects. Ecology 85: 383–397.

Letnic, M. and C.R. Dickman. 2005. The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, central Australia. Aust. Ecol. 30: 24–39.

Letnic, M., B. Tamayo and C.R. Dickman. 2005. The responses of mammals to la Niña (el Niño Southern oscillation) – associated rainfall, predation, and wildfire in central Australia. J. Mammal. 86: 689–703.

Lima, M., R. Juillard, N.C. Stenseth and F. Jaksic. 2001. Demographic dynamics of a neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climatic factors. J. Anim. Ecol. 70: 761–775.

MacMahon, J.A. 1981. Successional processes: comparison among biomes with special references to probable roles of and influences on animals. In: (D.C. West, H.H. Shugart and D.B. Botkin, eds.) Forest Succession. Concepts and Applications. Springer-Verlag, Berlin. pp. 277–304.

McKelvey, K.S. and D.E. Pearson. 2001. Population estimation with sparse data: the role of estimators versus indices revisited. Can. J. Zool. 79: 1754–1765.

Meserve, P.L., J.A. Yunger, J. Gutiérrez, L.C. Contreras, W.B. Milstead, B.K. Lang, K.L. Cramer, S. Herrera, V.O. Lagos, S.I. Silva, E.L. Tabilo, M.A. Torrealba and F.M. Jaksic. 1995. Heterogeneous responses of small mammals to an El Niño event in north-central semiarid Chile and the importance of ecological scale. J. Mammal. 76: 580–595.

Meserve, P.L., D.A. Kelt, W.D. Milstead and J.R. Gutiérrez. 2003. Thirteen years of shifting top-down and bottom-up control. BioScience 53: 633–646.

Monamy, V. and B.J. Fox. 2000. Small mammal successions is determined by vegetation density rather than time elapsed since disturbance. Austral Ecol. 25: 580–587.

Ordóñez, J.L. and J. Retana. 2004. Early reduction of post-fire recruitment of *Pinus nigra* by post-dispersal seed predation in different time-since fire habitats. Ecography 27: 449–458.

Parker, R.E. 1981. Estadística para biólogos. Ediciones Omega, Barcelona. pp. 136.

Pausas, J.G. and J.E. Keeley. 2009. A burning story: the role of fire in the history of life. BioScience 59: 593–601.

Perez-Cueva, A.J. 1994. Atlas climático de la Comunidad Valenciana. Consellería d'Obres Públiques, Urbanisme i Transports, València. pp. 205.

Pons, P. 2007. Consecuencias de los incendios forestales sobre los vertebrados y aspectos de su gestión en regiones mediterráneas. In: (J. Camprodon and E. Plana, eds.) Conservación de la biodiversidad, fauna vertebrada y gestión forestal. Segunda edición revisada y ampliada. Edicions Universitat de Barcelona, Barcelona. pp. 229–245.

Prodon, R., R. Fons and A.M. Peter. 1984. L'impact du feu sur la vegetation, les oiseaux et les micromammiféres dans diverses formations méditerranéennes des Pyrénées-Orientales. Premiers résultats. Rev. Ecol. 39: 129–158.

Prodon, R., R. Fons and F. Athias-Binche. 1987. The impact of fire on animal communities in mediterranean area. In: (L. Trabaud, ed.) The role of fire in ecological systems. SPB Academic Publishing, The Hague. pp. 121–157.

Reed, A.W. and N.A. Slade. 2008. Density-dependent recuitment in grassland small mammals. Appl. Ecol. 77: 57–65.

Reutter, B.A., V. Helfer, A.H. Hirzel and P. Vogel. 2003. Modelling habitat-suitability using museum collections: an example with three sympatric *Apodemus* species from the Alps. J. Biogeogr. 30: 581–590.

Santos, X., V. Bros and A. Miño. 2009. Recolonization of a burned Mediterranean area by terrestrial gastropods. Biodivers. Conserv. 18: 3153–3165.

Squeo, F.A., Y. Tracol, D. López, J.R. Gutiérrez, A.M. Cordova and J.R. Ehleringer. 2006. ENSO effects on primary productivity in Southern Atacama desert. Adv. Geosci. 6: 273–277.

Torre, I. 2004. Distribution, population dynamics and habitat selection of small mammals in Mediterranean environments: the role of climate, vegetation structure, and predation risk. PhD Thesis, Universitat de Barcelona, Barcelona. pp. 171.

Torre, I. and A. Arrizabalaga. 2000. Ecological aspects of small-mammal communities of Sant Llorenç del Munt i l'Obac Natural Park. In: IV Trobada d'Estudiosos de Sant Llorenç del Munt i l'Obac. Diputació de Barcelona, Barcelona. pp. 127–131 (in Catalan).

Torre, I. and A. Arrizabalaga. 2002. Effects of climate patterns on small-mammal population dynamics at Montseny. In: V Trobada d'estudiosos del Montseny. Monografies 33. Diputació de Barcelona, Barcelona. pp. 75–79 (in Catalan).

Torre, I. and M. Díaz. 2004. Small mammal abundance in Mediterranean post-fire habitats: a role for predators? Acta Oecol. 25: 137–143.

Torre, I., J.L. Tella and A. Arrizabalaga. 1996. Environmental and geographic factors affecting the distribution of small mammals in an isolated Mediterranean mountain. Z. Saugetierkd. 61: 365–375.

Torre, I., C. Flaquer and A. Arrizabalaga 2001. Distribution and abundance of small mammals in Montnegre i el Corredor Natural Park. In: III Trobada d'estudiosos del Montnegre i el corredor. Diputació de Barcelona, Barcelona. pp. 55–58 (in Catalan).

Torre, I., A. Arrizabalaga and M. Díaz. 2002. Ratón de campo (*Apodemus sylvaticus* Linnaeus, 1758). Galemys 14: 1–26.

Torre, I., A. Peris and L. Tena. 2005. Estimating the relative abundance and temporal activity patterns of wood mice (*Apodemus sylvaticus*) by remote photography in Mediterranean post-fire habitats. Galemys 17: 41–42.

Vieira, E.M. 1999. Small mammal communities and fire in the Brazilian Cerrado. J. Zool. (Lond) 249: 75–81.

Zar, J.H. 2010. Biostatistical analysis, 5th edition. Pearson Education International, Upper Saddle River, NJ. pp. 944.

Zwolak, R. and K.R. Foresman. 2007. Effects of a stand-replacing fire on small mammal communities in montane forest. Can. J. Zool. 85: 815–822.

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