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ORIGINAL PAPER

Ecological succession and habitat attributes affect the postfire response of a Mediterranean reptile community

Xavier Santos · José Manuel Poquet

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Abstract Wildfires are recognized as natural disturbances that have shaped landscape structure and ecosystem composition in many regions of the world. As ectotherms, many Mediterranean reptiles are expected to benefit from the thermal quality of open areas created by fires. However, not all the reptile species respond positively to this pattern. We have explored the response to fire of a Mediterranean reptile community in a protected area of the northeastern Iberian Peninsula. We visually searched for reptiles at 102 sites, including unburnt, recently burnt (2003), and old burnt (1985–1986) localities. The number of reptiles and species richness was higher at burnt sites, and both were related to several variables of the habitat structure. Accordingly, between the two most common species in recently burnt sites, *Podarcis hispanica* declined in old fire habitats whereas *Psammodromus algirus* did not. Snakes did not differ between burnt and unburnt areas, although the ambush predator viper *Vipera latastei* was found more frequently in unburnt habitats. Our results imply that there are different succession trajectories for Mediterranean reptile species according to their habitat preferences, life history traits, and dietary specialization. The study area has been drastically human-altered in the last 100 years by agriculture, pine reforestation, agricultural abandonment, and wildfires. These land use changes drastically alter the vegetation cover, favoring some reptiles and damaging others, and finally can promote local extinctions of sensitive species to habitat shifts.

Keywords Reptiles · Postfire response · Habitat selection · Land use · Mediterranean basin

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Introduction

The Mediterranean basin is widely recognized as one of the biodiversity hotspots in the world (Myers et al. 2000). Nevertheless, this region has been altered by human activities over the centuries (Bottema et al. 1990; Blondel and Aronson 1999). In this sense, the Iberian Peninsula has undergone drastic habitat transformations (e.g., urbanization, land abandonment, intensive agriculture, forestry, and fires) within small spatial scales and time periods (Lloret et al. 2002). All these activities have wreaked habitat transformation, fragmentation, and loss, affecting at least 15% of all endemic animal and plant species, currently threatened with extinction (Brooks et al. 2002). Wildfires are common natural perturbations in the Mediterranean region (Moreno and Oechel 1994; Rundel 1998; Trabaud and Prodon 2002), and human activities have increased their frequency and extent along the twentieth century (Lloret 2004). Wildfires impact animal communities by causing mortality directly (Wilson 1994; Whelan 1995) as well as indirectly by changes in postfire habitat structure (Wilson 1994; Whelan 1995; Brooks and Esque 2002). These changes have ecological consequences, in terms of

changing the thermal microclimate (Hurlbert 1969; Rice and Parenti 1978), exposure to predators, food availability (Evans 1984; Kaufman et al. 1990), and reproduction timing (Lillywhite and North 1974; Withgott 1996; Cavitt 2000).

In forest habitats, wildfire promotes the occurrence of new open areas and consequently facilitates the recolonization of open-space species (Herrando et al. 2003; Santos et al. 2009). Several ectothermal species take advantage of postfire conditions, colonizing new suitable thermal environments (Huey 1991), hence promoting a priori positive fire responses. This positive response has been observed in some reptile communities (e.g., Pianka 1996; Rugiero and Luiselli 2006). However, Caughley (1985) and Driscoll and Henderson (2008) reported that the response of reptiles to fire is not homogeneous within a single community. These authors recognized different succession trajectories for reptile species in Australian burnt areas, during the vegetation structure recovery. Some species rise in abundance just after fire whereas others need of many years for their recovery. Postfire changes in canopy and vegetation density succession can also be involved in local reptile extinction (Ballinger and Watts 1995; Jäggi and Baur 1999; Webb et al. 2005). These species-specific responses are related to habitat attributes and other environmental factors that vary across the postfire succession, favoring or harming species according to their requirements (Rugiero and Luiselli 2006).

The analyses of reptile responses to fire are informative for the conservation of these communities, poorly addressed in the Mediterranean region. The goal of our study is to examine the short-term response of a Mediterranean reptile community after a fire in terms of species richness and number of reptiles. The study has been conducted in a protected area affected by a big fire in 2003. We have sampled burnt and adjacent unburnt control sites to detect reptile species loss and gain after fire. Furthermore, for the two most common species, the objective has been to evaluate their responses to fire according to their habitat requirements. For these species, we also have compared their relative abundances in recent and old burnt sites (24 years after the fire) to analyze their postfire successional trajectories.

Material and methods

Study area

The study area is located inside the *Sant Llorenç del Munt i l'Obac* Natural Park, located in the NE Iberian Peninsula (Fig. 1). This is a 14,000-ha protected area characterized by a conglomerate landscape with Holm oak forest and Mediterranean shrubs, partially substituted by pine forest in peripheral areas of the park. The natural park has a long history of fires (667 fires registered between 1965 and 2003); however, the largest fire occurred in August 2003, when 4,500 ha on the eastern edge of the park were burnt (Fig. 1, zone C). Furthermore, in the western edge of the park, two big fires burnt in 1985 and 1986 (Fig. 1, zones A and B).

The reptile community in the Natural Park has been recorded by numerous visits made by park rangers and local herpetologists. Its reptile checklist has been reported and updated in several publications (Llorente et al. 1995; Pleguezuelos et al. 2002) and is available in 10×10 km UTM grid cells. Thirteen reptile species have been recorded in the park: one chelonian, six lizards, and six snakes.

Censuses methods

We made reptile censuses at 102 sites (Fig. 1) distributed in four habitat categories: (1) unburnt sites in Holm oak forests (n=17), (2) unburnt sites in pine forests (n=17), (3) old burnt sites (fires in 1985 or 1986, n=8), and (4) new burnt sites (fire in 2003, n=60). Prior to the fires, the majority of burnt sites were pine forests with Holm oak understory. These categories were selected to respond to the questions addressed in this work. We split unburnt sites in Holm oak and pine categories as these are the predominant forests in the Natural Park.

We recorded reptiles by two complementary methods: (1) reptile sightings during surveys searching for active specimens or those hidden inside vegetation or refuges. We surveyed each site twice, in spring and autumn 2007 during sunny and hot days, and each visit lasted 30 min. Reptiles were surveyed in an area of approximately 200-m diameter around the center of the sampling site. In each 200-m buffer, surveys were done in a zigzagging way in order to reduce resightings. Furthermore, in spring, we found mainly reproductive specimens whereas in autumn we often found juveniles. For this reason, the potential bias in the number of reptiles observed per site by resighting the same animals was much reduced. (2) At each sampling site, we located five pitfalls in a lineal transect separated 10 m from each other. Pitfalls were plastic containers of 10-cm diameter and 15-cm depth that effectively trapped lizards. Pitfalls were opened for 15 days every sampling period (spring and autumn) and checked every 2–3 days to report and release all reptiles trapped.

We also registered the macrohabitat (the area where reptiles were recorded) and microhabitat (the exact location where reptiles were recorded) of all the reptile specimens seen. Macrohabitat classes were described according to the presence of forest vs open sites; then, we defined the following classes: forest interior, forest edge, rocky area,

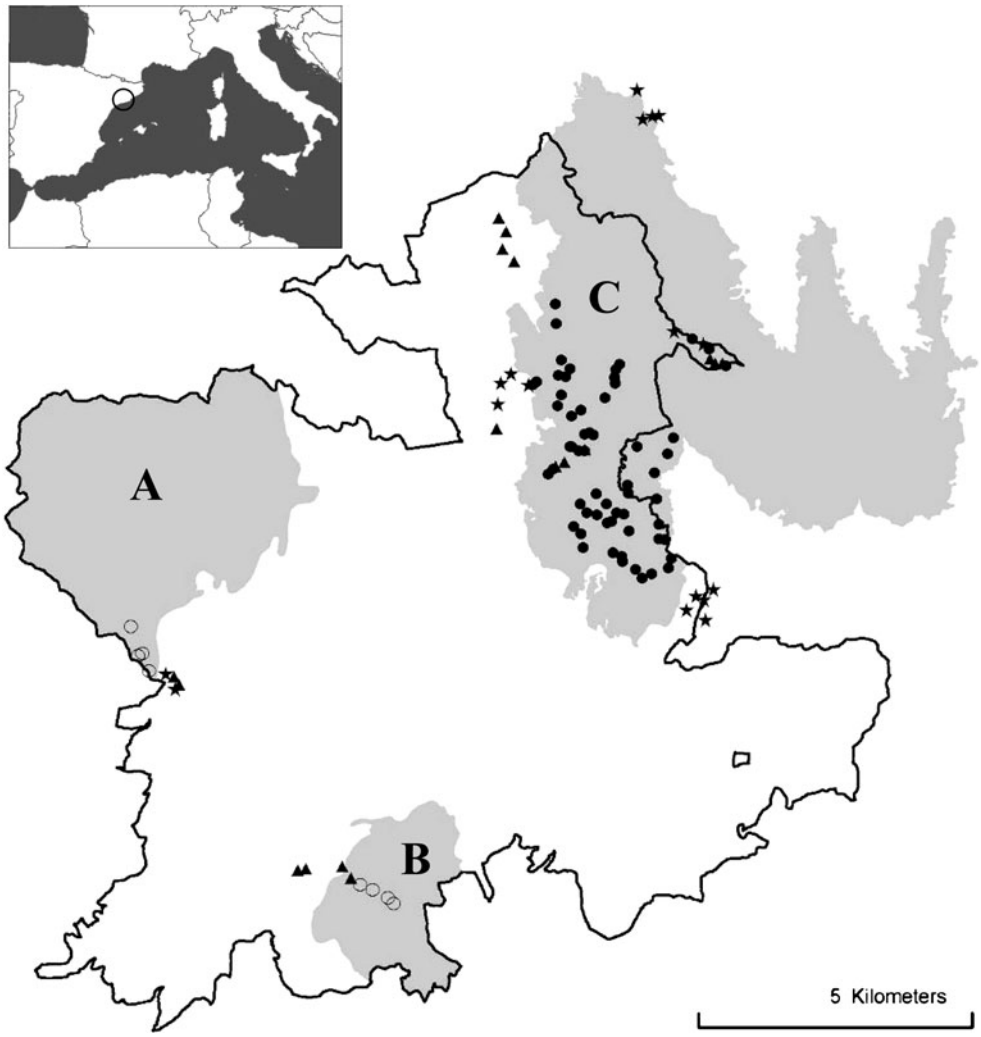

Fig. 1 Location of the study area in the NE Iberian Peninsula and the 2003 wildfire. *Symbols* represent the location of the 102 sampling sites as old fires (*open circle*), recent fire (*solid circle*), unburnt Holm oak (*solid triangle*), and unburnt pine (*stars*). Some unburnt sites, being inside the fire area, are unburnt isolated stands. The *black line* delimitates the *Sant Llorenç del Munt i l'Obac* Natural Park, and *gray areas* are the extent of the main fires of 1985 (*A*), 1986 (*B*), and 2003 (*C*)

burnt forest, and burnt forest edge. Microhabitat classes were grass, shrub, bare ground, and refuge (i.e., stone, dead trunk, and burnt branches).

Because of the sampling method described above, we found few snakes. For this reason, we also searched snakes at road trails within the park. Roads in unburnt and burnt areas were checked daily to collect dead snakes. Road trails were divided in 1-km stretches to compare statistically the number of snakes seen between unburnt and burnt areas.

We characterized habitat structure of the sampling sites by recording several vegetation and ground cover variables along a 50-m transect placed in the center of the site. The extent of several vegetation types (Holm oak, pine, oak, shrub, and grass) and ground cover variables (litter, refuges, bare ground, and wood) were recorded at points 50 cm apart along that transect. Thus, we recorded 100 points that characterized the abundance of vegetation and ground cover types at each site. We selected these variables due to their influence on the abundance and diversity of reptile communities (Ribeiro et al. 2009; Márquez-Ferrando et al. 2009).

Statistical procedures

Ground cover and vegetation variables were used to characterize habitat differences among sampling sites. We performed a nonmetric multidimensional scaling (NMDS) with the Bray–Curtis similarity measure to relate such habitat characteristics to the presence of fires (old and recent fires), as well as to unburnt forests. The NMDS is a robust nonparametric ordination technique that avoids the assumption of linear relationships among variables and allows the use of a wide range of data types and similarity measures (McCune and Grace 2002). In this case, only the relative distances between objects in the ordination are relevant to the interpretation of the underlying patterns (Quinn and Keough 2002). Thus, our sampling sites with similar habitat characteristics will be arranged close to one another within the NMDS plot, whereas sites with different habitat characteristics will be arranged separately. We used the software PC-Ord v5.14 (McCune and Mefford 2006) and its autopilot routine to conduct this analysis.

We performed several general linear model (GLM) to explore whether there were significant differences in species richness and number of reptiles according to the four habitat categories (Holm oak, pine, old burnt, and new burnt) and park zones (A, B, and C in Fig. 1). The latter factor was considered because of the clustered sampling selection due to the spatial distribution of old and new fires in the park (Fig. 1).

After differentiating between burnt (old and recent fires) and unburnt sites (types of forests) throughout their habitat attributes, we performed multiple regressions to detect the weightiest attributes for richness and number of reptiles. Similarly, we developed multiple regressions for the two most common species in the study area (the Spanish wall lizard *Podarcis hispanica* and the large Psammodromus, *Psammodromus algirus*). Previously, ground cover and vegetation variables were explored in order to detect and remove those much correlated variables (correlation coefficient $r \geq 0.8$). Afterwards, the best regression model in each case was selected following the best subset approach implemented in the STATISTICA v.7.1 software (Statsoft 2005). This approach avoids problems that stepwise methods present (Whittingham et al. 2006) and allows the selection of the best regression model by means of several information criterions (Burnham and Anderson 2002). Stepwise procedures explore a small subset of all possible regression models. In this sense, the order of entry (or deletion) of predictor variables and the number of candidate variables used can affect the final model selection. Partial F tests of individual predictors are used for variable inclusion and removing rules of the regression model. Thus, they can lead to biases in parameters, overfitting, and incorrect significance (Whittingham et al. 2006). We utilized the second-order Akaike's information criterion (AICc) to select the best regression model among all possible combinations of predictor variables (Burnham and Anderson 2002). This measure is recommended for situations where the sample size (n) compared to the number of parameters (k) is small ($n/k<40$). Due to our unbalanced design (i.e., unequal number of sampling sites between burnt and unburnt sites), we performed all GLM analyses (analyses of variance (ANOVAs) and multiple regressions) calculating the corresponding sums of squares with the type III method (Quinn and Keough 2002).

We used log-linear analyses to test the differences in the macrohabitat and microhabitat use by the two most common species (*P. hispanica* and *P. algirus*) in the study area. Log-linear analysis is a statistical procedure that tests the association between several categorical variables in a multidimensional contingency table. The algorithm used generates several models to test interactions between all variables and selects the least complex model that fit the data. Once the models have been chosen, the goodness of fit is evaluated by the maximum likelihood ratio chi-squared that compares whether the expected cell frequencies under the model significantly differ from the observed cell frequencies (i.e., in a good model, p will not be significant). The results are interpreted by regarding the odds ratio values among categories in the expected values of the marginal tables. GLM and log-linear analyses were performed with the STATISTICA v.7.1 software (Statsoft 2005).

The spatial distribution of the burnt and unburnt sites was constrained by the location of the old and recent fires, as well as by the presence of Holm oak and pine forests. The spatial pattern of species richness and total number of reptiles were explored by a distance-based autocorrelation analysis performed with Passage ver. 1.1 (Rosenberg 2004). We constructed 25 distance classes of unequal length, setting constant the number of site pairs (n=200) being correlated. We performed a correlogram for the species richness and total number of reptiles, and spatial classes were defined by progressive distance between pairs of sites. Moran's I coefficients of spatial autocorrelation was calculated for each distance class and the significance level achieved by Monte Carlo method with 2,000 permutations. The significance of autocorrelation coefficients was corrected by a Bonferroni procedure due to the lack of independence of the distance classes (see Sánchez-Zapata et al. 2003).

Results

During our field sampling and road trips, we found specimens of 12 out of 13 species previously recorded in the park (Table 1). The only undetected species was the Spanish terrapin *Mauremys leprosa*, since the sampling design was not adequate to see such reptiles as this chelonian inhabiting water bodies. Among lizards, only two species, *P. hispanica* and *P. algirus*, can be considered common in the Natural Park, although the ocellated lizard *Timon lepidus* has been found commonly at burnt sites.

The two-dimensional ordination given by the NMDS analysis (13.11% stress level) showed clear differences among burnt and unburnt sampling sites (Fig. 2). The first NMDS axis was positively correlated with the abundance of bare ground (r=0.84) and negatively correlated with the abundance of litter (r=−0.82) and pines (r=−0.76). On the other hand, the second NMDS axis was highly correlated with the abundance of Holm oaks (r=0.90) and litter (r=0.87). Thus, most of burnt sites were located on the positive axis 1, recently burnt sites being the most concentrated. Unburnt sites were widespread along the axis 1 negative side, with a clear gradient from pine to Holm oak forest sites along axis 2 (Fig. 2).

Table 1 Mean and total (in brackets) number of records per site of reptile species found during the sampling in burnt and unburnt sites at *Sant Llorenç del Munt i l'Obac* Natural Park

Lizard species	Code	US, n=34	NBS, n=60	OBS, n=8	TR, n=102
Tarentola mauritanica	TAM	0.06 (2)	0.02 (1)	0.00 (0)	0.03 (3)
Anguis fragilis	AF	0.03 (1)	0.00 (0)	0.00 (0)	0.01 (1)
Podarcis hispanica	PH	0.53 (18)	3.60 (216)	0.13 (1)	2.32 (237)
Psammodromus algirus	PSA	1.47 (50)	2.40 (144)	6.13 (49)	2.38 (243)
Psammodromus hispanicus	PSH	0.00 (0)	0.02 (1)	0.00 (0)	0.01 (1)
Timon lepidus	TL	0.06 (2)	0.27 (16)	0.00 (0)	0.18 (18)
Snake species		UR n=38	BR n=19		
Malpolon monspessulanus	MM	0.34 (13)	0.42 (8)		
Rhinechis scalaris	RS	0.18 (7)	0.26 (5)		
Coronella girondica	CG	0.05 (2)	0.05 (1)		
Natrix natrix	NN	0.11 (4)	0.11 (2)		
Natrix maura	NM	0.05 (2)	0.11 (2)		
Vipera latastei	VL	0.26 (10)	0.05 (1)		

Type of sites: unburnt (US), recently burnt (NBS), old burnt (OBS), and total number of records (TR) in the 102 sites sampling. For snakes, mean and total number records in unburnt road transects and sites (UR) and records in burnt road transects and sites (BR) were pooled

The total number of reptiles and species richness showed significant differences between habitat categories (total number of reptiles: $F_{3,\ 96}$=15.59, p<0.00001; species richness: $F_{3,\ 96}$=9.61, p=0.00001). Scheffé post hoc comparisons indicated that differences were between burnt and unburnt sites (p<0.05). Furthermore, there were marginal differences for species richness between old and recently burnt sites (p=0.06) although there were no differences for the number of reptiles (Fig. 3). In contrast, the GLM did not find differences between the three zones for the number of reptiles and species seen per site. This result suggests that, although the sampling was clustered by the location of the fires, differences were not related to the spatial distribution of the sites.

We found significant differences in the number of reptiles seen or trapped among the four site categories (visual, ANOVA $F_{3,\ 98}$=13.90, p<0.00001; trapped, $F_{3,\ 98}$= 4.14, p=0.008). Scheffé post hoc comparisons indicated

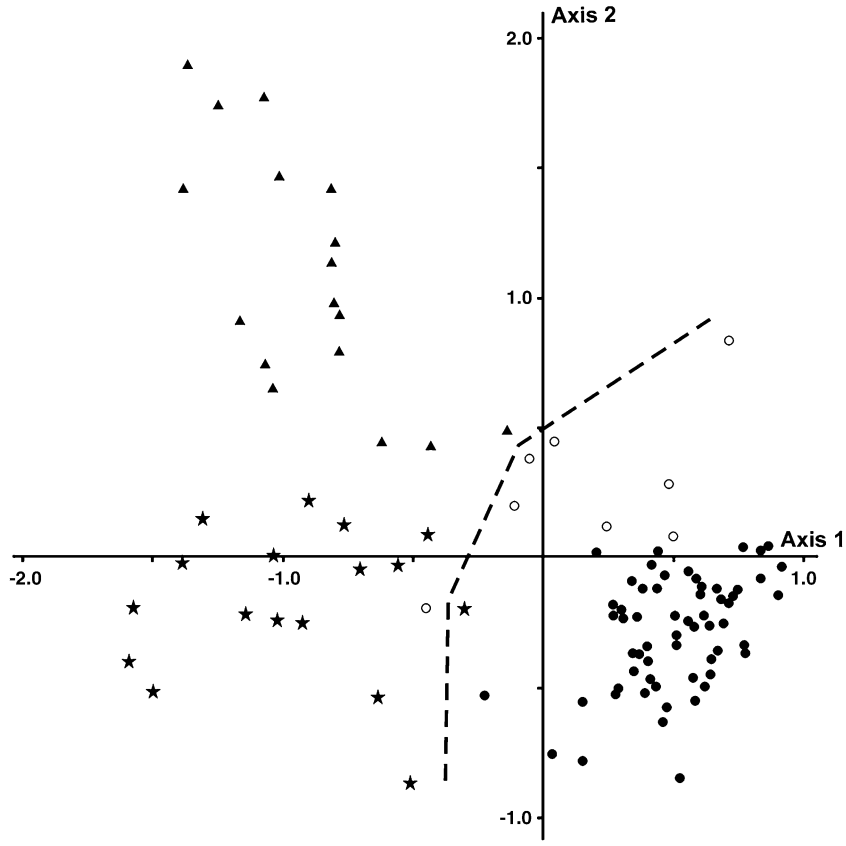

Fig. 2 NMDS two-dimensional ordination of sampling sites based on their vegetation structure and ground cover characterization. *Dashed line* separates burnt (*right*) from unburnt (*left*) sites. Moreover, burnt sites are classified into old (*open circles*) and recent (*solid circles*) fires, whereas unburnt sites are classified into Holm oak (*solid triangles*) and pine (*stars*) forests

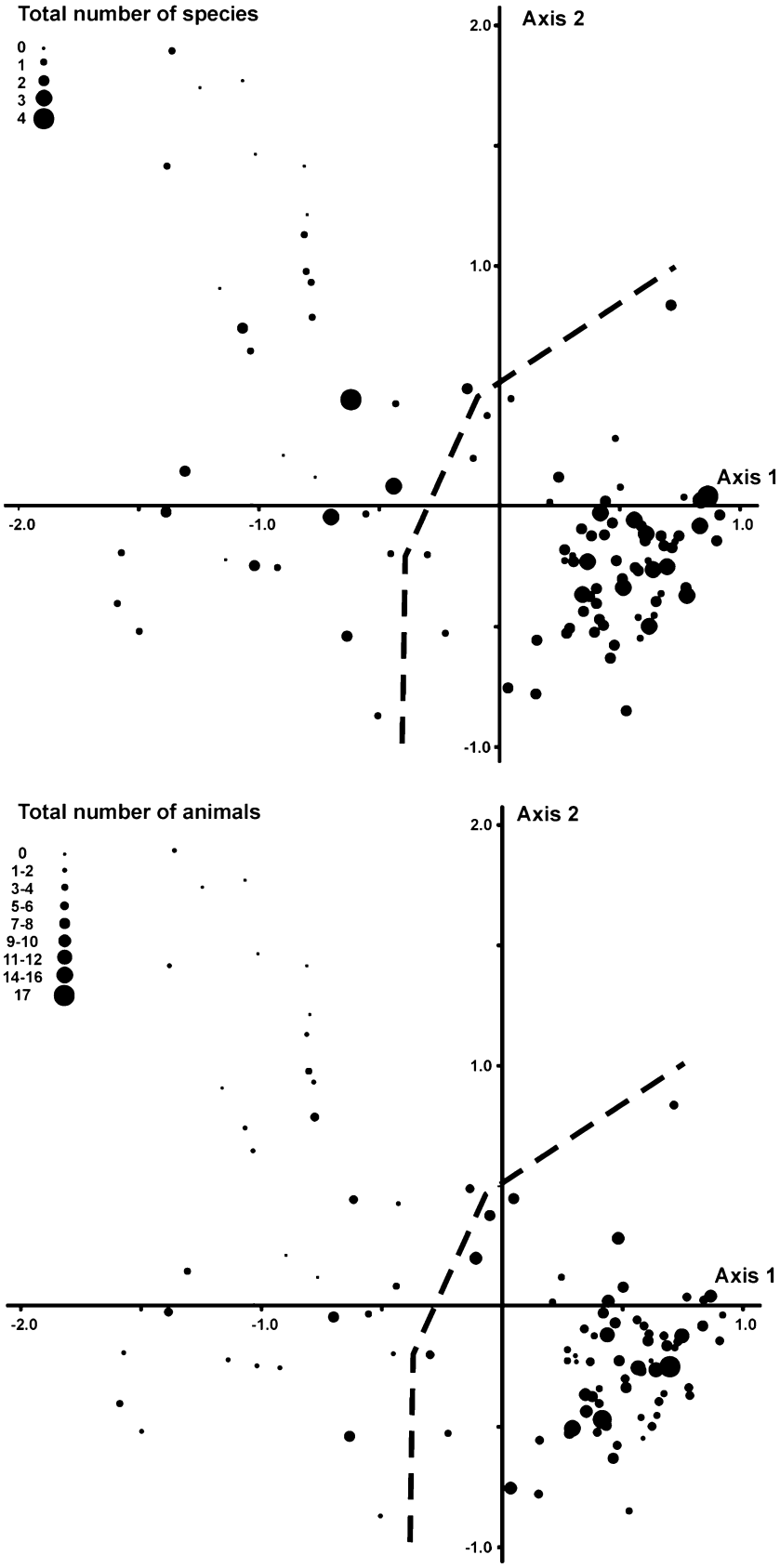

Fig. 3 NMDS two-dimensional ordination of sampling sites where the *symbol size* is proportional to the size of the total number of species (*up*) and the total number of animals (*down*). *Dashed line* separates burnt (*right*) and unburnt (*left*) sites

in both sampling methods that the number of reptiles was higher in burnt than in unburnt sites.

We did not find spatial autocorrelation of the total number of reptiles seen per site as there were no significant Moran's I coefficients for low-distance classes (Electronic Supplementary Material Table S1 and Figure S1). In contrast, we find spatial autocorrelation of the species richness as the closest sites (distances between sites up to 816 m) showed significant positive Moran's I coefficients (Electronic Supplementary Material Table S2 and Figure S2).

The best regression model for total number of reptiles seen (AICc = 213.57) showed that, among all vegetation and ground cover variables, pine, litter, and wood had significant effects. These three variables explained 37% of the variation of the total number of animals (number of reptiles=5.46−0.25 pine−0.32 litter+0.26 wood, $F_{3,\ 98}$= 21.06, p<0.001, r^2=0.37). On the other hand, the best regression model for species richness (AICc=−52.78) showed that litter and grass had significant negative effects on the total number of species, explaining 29% of its variation (species richness=2.28−0.53 litter−0.24 grass, $F_{2,\ 99}$=21.97, p<0.001, r^2=0.29).

One of two most common reptile species *P. hispanica* declined from recent to old burnt sites (student t test, t= 3.02, df=66, p=0.004) whereas *P. algirus* increased (t= −6.67, df=66, p<0.00001; Table 1). These two lizard species presented different requirements regarding the vegetation composition and ground cover structure. The best regression model for *P. hispanica* (AICc=170.01) showed its abundance to be positively determined by ground cover structures: refuges, bare ground, and wood (*P. hispanica*=−0.77+0.30 refuges+0.20 bare ground+0.44 wood, $F_{3,\ 98}$=26.46, p<0.001). These variables explained 43% of *P. hispanica* variation (r^2=0.43). On the other hand, although the best regression model for *P. algirus* (AICc= 123.2; *P. algirus*=1.91−0.27 pine+0.24 shrub−0.17 refuges, $F_{3,\ 98}$=6.76, p<0.001, r^2=0.15) involved one ground cover variable (refuges), this had no significant effect on *P. algirus* abundance ($F_{1,\ 98}$=3.41, p=0.068). Those variables that mainly determine *P. algirus* abundance were two vegetation composition variables (pine $F_{1,\ 98}$=7.38, p=0.008; shrub $F_{1,\ 98}$=6.14, p=0.015).

The log-linear analysis showed significant interactions among macrohabitat types, the presence of the two commonest species (*P. hispanica* and *P. algirus*), and the time since the last fire occurred (final model maximum likelihood ratio chi-squared, χ^2=3.12, p= 0.93). The highest odds ratio score (odds ratio>2) of two-variable marginal tables showed that *P. algirus* preferred forest-interior and forest-edge macrohabitats. Similarly, log-linear analysis also showed significant interactions, taking into account microhabitat types (final model maximum likelihood ratio chi-squared, χ^2=2.71, p=0.84). The highest odds ratio scores (odds ratio>2) of the two-variable marginal tables showed that *P. algirus* preferred grass and shrub microhabitats, and *P. hispanica* preferred refuges.

In agreement to the log-linear analyses, the percentage of *P. hispanica* and *P. algirus* recorded in different macrohabitats showed interspecific differences at unburnt sites, i.e., forested habitats for *P. algirus* and rocky habitats for *P. hispanica* (Fig. 4a). In contrast, differences were lower at burnt sites, probably due to the simplification of the habitat. The microhabitat preferences of *P. algirus* and *P. hispanica* in burnt and unburnt sites were clearly different and evidenced their ecological requirements: *P. algirus* selected shrub whereas *P. hispanica* selected refuges (Fig. 4b).

We found 57 snakes of six species, 19 in burnt and 38 in unburnt localities, combining samplings and road trail records (Table 1). The five colubrid species apparently inhabited both areas, although the small samples sizes preclude statistical comparisons. In contrast, the only viper in the park, the Lataste's viper *Vipera latastei* was found almost only in unburnt localities. Considering only the number of snakes found in 42 stretches of 1 km long in burnt and unburnt areas surveyed, we found no differences in the number of snakes (unburnt 23 transects, burnt nine transects, Mann–Whitney U test U=94.5, p=0.70).

Discussion

This study presents several pieces of evidence in favor of the variable postfire response of the Mediterranean reptile community studied, some species increasing in burnt (*P. algirus*) or only in recently burnt areas (*P. hispanica*) and others decreasing (*V. latastei*). These results may be informative for conservation issues and habitat restoration programs for reptiles in Mediterranean areas. Overall, there is an increase of reptiles in burnt localities, in agreement with other works that have demonstrated enhanced reptile populations in burnt habitats (e.g., Bury 2004). Burnt and unburnt habitats differ in terms of habitat structure and availability of open areas (Fig. 2), and thus the large number of reptiles found at burnt sites should be related to the quality of the habitat (see also Valentine and Schwarzkopf 2008). The higher number of reptiles collected in pitfalls at burnt sites can be caused by their increased mobility on open areas. However, differences in the number of reptiles were observed with both sampling methods (visual trials and pitfalls), thus sustaining the statement that the number of reptiles increased in burnt pine forests.

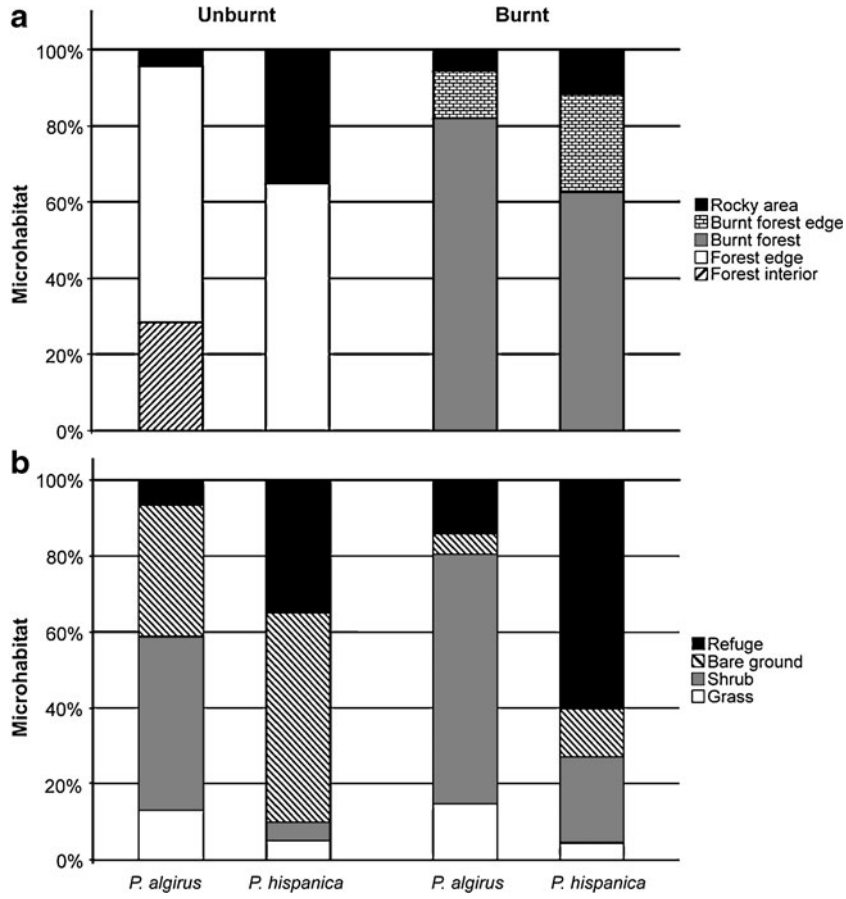

Fig. 4 Percentage of *P. hispanica* and *P. algirus* in **a** macrohabitat and **b** microhabitat types in burnt and unburnt sites

The extent of litter negatively affects species richness, and this result should reflect the general difficulty of reptiles to thermoregulate inside a dense canopy (Huey 1991). Our results are compatible with the thermal dependence hypothesis for reptiles as their richness (Moreno-Rueda and Pizarro 2007) and distribution (Aragón et al. 2010) are strongly associated to temperature in the Mediterranean region. However, this does not apply in other parts of the world different to the Mediterranean biome, particularly tropical and desert areas (Kearney et al. 2009). The extent of grass also negatively affected species richness. In other words, within burnt sites, those with a high extent of grass have lesser reptile species than those without grass. An expansion of short-lived seeding plant species such as grass is a typical trend in early postfire succession (Lloret 2004); however, the commonest reptiles in the park, *P. hispanica* and *P. algirus*, did not make use of grassy habitats either at burnt (Fig. 4) nor unburnt sites (Pérez-Mellado 1982). This pattern is in fact general for Mediterranean areas where only a few species are grassy vegetation specialists (except skinks of the genus *Chalcides*, Rugiero and Luiselli 2006).

All reptile species living in the Natural Park do not follow the same postfire response, this conclusion confirming previous findings in Australia (Caughley 1985; Driscoll and Henderson 2008) and USA (Perry et al. 2009). Several of our results support this conclusion:

1. All lizards previously reported in the Natural Park were detected during this survey. However, within lizards, there were also interspecific differences in the successful colonization of burnt areas. For example, the Moorish gecko *Tarentola mauritanica* did not colonize burnt habitats regardless of the presence of adequate microhabitats (Hódar et al. 2006). Species living inside the forest (i.e., the slow worm *Anguis fragilis*) was not recorded at burnt sites although was frequently killed on roads crossing unburnt areas within the Natural Park (authors, personal observation).
2. Despite of the thermoregulatory quality of burnt habitats for reptiles, the number of snakes seen did not differ between roads crossing adjacent burnt and unburnt areas. This result could be related to some ecological life history constraints of snakes that did not affect lizards. Specialists in some ecological traits and low reproductive output, snakes are particularly sensitive to anthropogenic habitat disturbance (see a review in Webb and Shine 1998). Although many ecological

features of snakes are unknown, many species combine several traits such as low fecundity, retarded sexual maturity, and small population size, making them vulnerable to extinction (Webb et al. 2002). Within snakes, specialist species in the habitat use are more threatened than generalist species (Segura et al. 2007), and ambush predators snakes are more commonly threatened than active foragers (Reed and Shine 2002). Within the snake assemblage in the Natural Park, *V. latastei* is the only ambush predator and the most ecological specialist (Santos et al. 2006), factors that probably would explain why it was found more frequently in unburnt than in burnt habitats (Table 1). The low numbers of snake observations suggest the need of snake-specific capture techniques in future studies to analyze explicitly the response of these species to fire.

3. Between the two most common species in the Natural Park, there were also clear differences in their postfire trajectories. Both lizards are good short-term colonizers of burnt areas, with dense populations at some recently burnt sites (Santos, personal observation). However, in old fire sites, *P. hispanica* clearly declined whereas *P. algirus* did not. The low numbers of *P hispanica* in old burnt sites could be a location effect as the sampling design is spatially clustered due to the distribution of old and recent fires (Fig. 1). However, GLM analyses did not find differences in species richness between eastern and western areas, whereas old and recent fires marginally did. These differences between the commonest reptiles are similar to those reported in other postfire succession studies (Pianka 1996; Letnic et al. 2004; Driscoll and Henderson 2008). In our case, *P. hispanica* and *P. algirus* differed at macrohabitat and microhabitat scales and also with regard to burnt and unburnt sites. At unburnt sites, *P. hispanica* and *P. algirus* are known to be spatially segregated at both macrohabitat and microhabitat scales (Pérez-Mellado 1982). In recent fire sites, despite a simplification of the habitat structure, both species are abundant and remain spatially segregated, especially in their microhabitat preferences (Fig. 4b). In old fire sites (25 years after fire), *P. hispanica* becomes uncommon probably because of vegetation recovery whereas *P. algirus* remains abundant. This conclusion reflects that habitat quality is ephemeral for species with special habitat requirements as *P. hispanica* (i.e., specialists of first stages in the ecological succession, Buddle et al. 2006). In fire-suppressed landscapes, vegetation density and cover increase and habitat heterogeneity declines, negatively affecting biodiversity in several groups (Conway and Kirkpatrick 2007; Moreno-Rueda and Pizarro 2007) including reptiles (Webb et al. 2005).

In addition to the increase of canopy cover during postfire succession, the availability of shelter sites underlies the successful recovery of reptile populations at burnt habitats. In fact, several examples of habitat restoration for reptiles are based on the addition of artificial refuges in degraded habitats (e.g., Zappalorti and Reinert 1994; Castilla and Swallow 1995; Webb and Shine 2000; Márquez-Ferrando et al. 2009). The increment of vegetation during succession closes shelters or makes them unattractive to many species, and the scarcity of refuges negatively affects reptiles at the population and community levels (Goode et al. 2005). Accordingly, in our study, *P. hispanica* was common under refuges at burnt sites (60% of records, Fig. 4b) whereas only 35% of observations in unburnt sites were due to the reduction of these microhabitats in unburnt habitats. In burnt sites with scarcity of shelters (rocks and walls), *P. hispanica* was seen frequently on dead trees where they have not been removed (Santos, personal observation). In consequence, logging can impact the viability of species such as *P. hispanica*, as it has been documented in other species (Lindenmayer et al. 2004; Kavanagh and Stanton 2005; Herrando et al. 2009). Nevertheless, logging is the most widespread practice in the Mediterranean Basin (Haim and Izhaki 2000).

The Mediterranean Basin has been shaped by humans for millennia (Blondel and Aronson 1999). Several pastoral and agricultural activities have sustained a diverse array of biological communities which have developed a strong preference for seminatural habitats (Moreira and Russo 2007). For this reason, postfire response of a Mediterranean reptile community should be analyzed in light of the historical land use changes made in the area studied. In the early twentieth century, the study area was dominated by vineyards with very scarce vegetation (Electronic Supplementary Materials Figure S3a). After the *Phylloxera* plague, fields were abandoned and naturally replaced by pine forest and Holm oak undergrowth (Fig. S3b). Agricultural abandonment in recent decades has completed the forest recovery of the area, although the fire of 2003 altered the landscape structure again (Fig. S3c). It is likely that this historical transformation of the land use and vegetation cover had selectively affected species with high sensitivity to local habitat changes such as Mediterranean reptiles (Ribeiro et al. 2009). Then, this factor should be taken into account to analyze the response of reptiles to disturbances in human-altered habitats by comparing historical reptile records and land changes in long-term surveyed areas.

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