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The role of fire history, land-use, and vegetation structure on the response of Mediterranean lizards to fire

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ABSTRACT

Fire is a critical component of terrestrial ecosystems and essential to understand the composition and diversity of communities in fire-prone regions. Nevertheless, fire does not act alone, and other factors such as land-use type and vegetation structure can also operate at different scales, prompting the response to fire of ectotherm communities such as reptiles. We have evaluated the influence of environmental factors on the abundance, diversity, and richness of reptile communities in Serra da Estrela Natural Park (northern Portugal), at both the landscape and micro-habitat scales. In spring 2014 and 2015, 20 transects were surveyed eight times, the vegetation structure and composition were measured, and the extent of land-use types around each transect calculated in this Mediterranean community. At the landscape scale, reptile abundance was higher in natural woodlands and more complex habitats (higher vegetation heterogeneity and plant richness), and reptile evenness was affected by vegetation heterogeneity and time since fire. By contrast, species richness was not related to any environmental factor measured in this study. Only two lizard species were common in the park, *Psammodromus algirus* and *Podarcis guadarramae*. Their relative abundances increased with contrasting habitat variables as the former is a ground-dwelling lizard specialist that prefers heterogeneous (unburnt) habitats and the second is a rock lizard that selects open (burnt) stands. At the micro-habitat scale, the probability of reptile presence, reptile abundance, and reptile richness increased with plant richness and decreased with tree cover. This study highlights the importance of several environmental factors, that operate from micro-habitat to landscape scales to understand the response of reptiles to fire.

1. Introduction

Fire is a fundamental driver of many terrestrial biomes, including Mediterranean type ecosystems (Bond et al., 2005; Bowman et al., 2009, Pausas and Keeley, 2009), and many species have adaptive traits that enable them to persist in these fire-prone habitats (Keeley et al., 2012, Santos and Cheylan, 2013). In the Mediterranean basin, vegetation structure (e.g. heterogeneity, plant diversity, vegetation cover), land-use and fire history (e.g. fire recurrence and time since fire), synergistically interact and shape species habitats (Blondel et al., 2010), with important consequences for the diversity and abundance of different animal species (Moreira and Russo, 2007), but particularly for taxa with low-dispersal ability such as reptiles (Santos et al., 2014; Badiane et al., 2017). Reptiles are sensitive to alterations in habitat attributes such as vegetation structure (e.g. heterogeneity and cover of the different vegetation strata) because they are ectotherms, narrow-ranging species, and characterized by low vagility and dispersal rates (Huey, 1982; Valentine and Schwarzkopf, 2008; Azor et al., 2015).

There is evidence that fire history characteristics (e.g. fire recurrence and time since fire) are not the only drivers affecting reptile communities in fire-prone ecosystems, and other processes, like habitat structure, biogeographic affinity, and food availability, operating at different spatial scales, might be equally important (Driscoll and Henderson, 2008; Pastro et al., 2013; Ferreira et al., 2016b). Besides the direct impact of fire on animals (i. e. mortality; Smith et al., 2001; Couturier et al., 2011), shifts in vegetation along postfire successional stages are important in order to characterize reptile communities in fire-prone ecosystems (Driscoll et al., 2012; Santos and Cheylan, 2013; Smith et al., 2013; Santos et al., 2016). The complex relationship between fire and vegetation structure (Nimmo et al., 2014) makes it

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advisable to incorporate vegetation factors into fire-history models to better understand the response of reptiles to fire (Santos et al., 2016).

At the landscape scale, vegetation heterogeneity (Nimmo et al., 2012) and land-use type can be key factors explaining total abundance and species richness in reptile communities (Ribeiro et al., 2009; Azor et al., 2015; Santos et al., 2016). At the micro-habitat scale, characteristics such as vegetation cover or plant richness can be important because they influence the habitat by affecting the availability of shelters, food, or sun exposure (Webb and Shine, 1998; Kim and Holt, 2012; Elzer et al., 2013). These factors can operate in concert with fire history to shape reptile communities in fire-prone ecosystems according to the specific life-history traits of each reptile species (Ferreira et al., 2016b; Santos et al., 2016). For this reason, landscape- and micro-habitat-scale factors have to be integrated to attain a comprehensive view of the composition of reptile communities in fire-prone ecosystems.

This study was conducted in the Serra da Estrela Natural Park (northern Portugal), and performed at two different scales: at the landscape scale, we analyzed the effect of fire history (fire recurrence and time since fire), vegetation heterogeneity, and land-use (main land-use type and land-use diversity) on the reptile abundance, richness and evenness. At the micro-habitat scale, we analyzed the role of plant richness and vegetation cover (tree, shrub, and herbaceous cover) on the probability of reptile presence, reptile abundance and evenness.

We hypothesize that species richness, reptile abundance and evenness are higher in natural areas (woodlands and scrublands) and in areas with higher land-use diversity (landscape scale) as well as in locations with higher plant diversity and lower tree cover (micro-habitat scale). Furthermore, we also expect that fire history (number of fires and time since fire) will affect the reptile community by altering the habitat structure (Ferreira et al., 2016b; Santos et al., 2016).

2. Materials and methods

2.1. Fire regime in Portugal and in the study area

Portugal has the highest fire incidence in Europe (Nunes et al., 2005; Catry et al., 2006; Oliveira et al., 2012), and fire is considered one of the most important agents of landscape change (Silva et al., 2011). Fire frequency and intensity have increased remarkably since the 1960s due to a combination of socioeconomic and environmental conditions such as rural abandonment, and conversion of marginally productive agriculture to eucalypt and pine plantations (Moreira et al., 2001, 2011; Fernandes et al., 2013). The climate is warm temperate characterized by hot, dry summers and cool, wet winters; likewise, natural vegetation is typically evergreen, resistant to drought, and pyrophytic (Nunes et al., 2005). Thus, both socioeconomic and environmental conditions lead to a high accumulation of fuel leading to a high risk of fire (Moreira et al., 2001, 2009). Catry et al. (2009) concluded that human activities were the primary cause of wildfires since about 60% of ignitions have occurred in areas of high population density and close to roads.

Serra da Estrela is a mountainous area located in the east-central region of Portugal (Supplementary materials Fig. S1), characterized by a high elevational gradient (250–1993 m). The mean annual rainfall ranges from 1000 mm in the lowest elevations to approximately 2500 mm at highest elevations (SNIRH, 2015), and the mean annual temperature ranges from 22 °C to 4 °C at the lowest and highest elevations, respectively. The Serra da Estrela Natural Park (hereafter SENP) is the largest protected area in Portugal (1.0106 km^2) and encloses most of this mountain area. The park is a landscape mosaic shaped by a long fire history (Connor et al., 2012) and multiple land uses (including woodlands, scrublands, coniferous plantations, and agriculture areas) arranged across an elevational gradient.

The reptile community at the SENP is composed of 20 species, i.e. 12 lizards and 8 snakes (Lesparre and Crespo, 2008; Supplementary materials Table S2), from both Mediterranean and Atlantic origins (following Sillero et al., 2009).

2.2. Site selection and environmental characterization

Twenty sites were selected across a fire-history gradient (Supplementary materials Fig. S1). The fire history was provided by the Instituto da Conservação da Natureza e Florestas (ICNF). Each site was characterized according to two fire-history variables, time since last fire (ranging from 0 to > 40 years) and fire recurrence (number of fires, ranging from 0 to 6 fires over a period of 40 years; Supplementary materials Table S3). Sites were a minimum of 600 m apart (mean distance and standard deviation between pairs: 17 ± 10 km) and sites with a similar fire history were placed as far as possible from each other to avoid spatial autocorrelation.

Land-use was examined in 200-m buffers around each transect. Raw data were obtained from the Portuguese land-cover map (IGP, 2008) and reclassified to five land-use types: monocultures (pine or eucalyptus plantations), agriculture fields, natural woodlands, scrublands, and urban areas (Supplementary materials Fig. S1). Our interest was in the effects of these major land-use types on the abundance and diversity of Mediterranean reptiles (Ribeiro et al., 2009; Azor et al., 2015). We calculated the land-use diversity as the Simpson diversity index of all land uses within the 200-m buffer, and according to the commonest land-use types (i.e. monoculture, scrubland and natural woodland; Supplementary materials Fig. S4). The spatial distribution of the transects by land-use classification was clustered, with the majority of monocultures located on the western part and scrubland areas on the eastern part of the study area.

Elevation was considered during site selection due to its influence on reptile presence and distribution (McCain, 2010; Kutt et al., 2011). Transects were selected within the elevational range of 250–1250 m, to avoid sampling on mountaintops that are characterized by the presence of alpine reptile species (i.e. *Iberolacerta monticola* and *Coronella austriaca*) and the absence of fires.

To characterize vegetation structure and heterogeneity, each transect was divided into 20-m sections. In each section, the vegetation within 2 m on either side of the transect (“left” and “right”) was identified to the species level (only for perennial species, because their constancy over the sampling period of the study). For each transect, the vegetation heterogeneity was accessed through a similarity index (Baselga et al., 2007) ranging between 0 and 1, with values approaching 1 indicating greater dissimilarity (higher vegetation heterogeneity). This index provided an estimate of overall compositional heterogeneity among sections, regardless of differences in species richness. For this, we divided the total number of plant species in each 20 m section by the sum of the minimum values of species not shared between each pair (left and right) of sections. For each transect and at each 20-m section, we described the vegetation structure according to the extent of tree, shrub, and herbaceous layers, ranging each layer from 0% to 100% cover.

2.3. Reptile sampling

Transects were placed on trails to facilitate reptile detectability (see a similar procedure in Santos and Cheylan, 2013), with an average length of 1 km (SD: 159 m; range 770–1250 m) and were as linear as possible to avoid recording the same individuals along the transect. Between May and September of 2014, and May and June of 2015, each transect was visited eight times (four visits in spring 2014, 1 visit in autumn 2014, and 3 visits in spring 2015) for 45 min each, walking slowly at a constant speed. During each visit, all transects were surveyed within 4–5 days, and visits were at least a week and a half apart. The surveys were made on sunny days and during the hours of reptile activity (from 09h00 to 18h00). Searches included open sites and we also turned rocks and other refuges to maximize observations (Santos and Cheylan, 2013; Santos et al., 2016). All the reptiles recorded were identified to the species level, except the two skink species of the genus *Chalcides* (*C. striatus* and *C. bedriagai*), that were pooled into one group because they were difficult to distinguish during the surveys. All reptile sightings were georeferenced and the perpendicular distance to the transect was noted to access differences in detectability (e.g. due to differences in vegetation cover; see a similar treatment in Santos and Cheylan, 2013). We found no difference in reptile detectability related to time since fire ($P = 0.27$) or fire recurrence ($P = 0.35$).

2.4. Statistical analysis

For statistical analyses, we used "Visit" as the reptile sampling unit (20 transects $*$ 8 visits per transect $= 160$ sampling units) to model the total abundance of reptiles, as well as the abundance of the two most common reptile species, the lizards *Psammodromus algirus* and *Podarcis guadarramae*. Due to the low detectability of many reptile species, we pooled the data of visits into two "Year" units (20 transects $*$ 2 years $= 40$ samples), since four visits per year more accurately describe the reptile richness and diversity of the transects.

The community metrics examined include the total number of reptiles (abundance), the number of different reptile species observed (richness), and the Pielou's evenness as a measure of reptile diversity. Evenness quantifies the degree of numerical equality among reptile abundances in each sampling unit; therefore, higher evenness scores indicate more complex (heterogeneous) communities in terms of species composition and relative abundances.

At the landscape level, we tested the effects of the fire recurrence and time since fire (fire history), vegetation heterogeneity, plant richness, land-use type (monocultures, scrublands, and natural woodland) and land-use diversity on the three reptile community metrics. Although recent studies have suggested that General Additive Models (GAM) are more suitable than General Linear Models (GLM) for modelling the response of reptile species to environmental factors and fire (Hu et al., 2013, 2016; Santos et al., 2016), a preliminary test with our data indicated a linear model would be more suitable (smoothing terms in GAMs had $edf = 1$; Thomas et al. 2015). Thus, we used Generalized Linear Mixed Models (GLMM) with Poisson distribution (for reptile abundance and species richness) and Gaussian distribution (for diversity) and used "Visit" (for reptile abundance) and "Year" (for species richness and evenness) as random effects. Altitude was also included as a random effect using three levels of elevation (< 600, 600–900 and > 900 m). The levels of elevation were chosen according to the climate in the PNSE. Below 900 m, the climate is typically meso-Mediterranean, while between 900 and 1250 m the climate is supra-Mediterranean. We divided the meso-Mediterranean climate level to have a similar number of transects in each level. The vegetation composition also changes along this altitude gradient.

Fire tends to modify the composition of reptile communities (Santos and Cheylan, 2013). For this reason, we computed differences in reptile communities (using species-specific abundance data) between pairs of sampling transects using the Bray-Curtis similarity index. This index allowed a comparison of the number and abundance of reptile species shared between transects. From the pairwise similarity matrix, we performed an Analysis of Similarity, ANOSIM (Primer, 2001), which gives a general R-value and allows comparisons in reptile communities between transect classes. For the ANOSIM, transects were classified according to the dominant land-use type (monoculture, scrubland and natural woodland), and time-since-fire interval, namely recently burned (< 5 years since the last fire), medium (5–10 years since the last fire), long (10–20 years since the last fire) and long-unburned (> 20 years since the last fire) (Supplementary materials Table S3). GLMM and ANOSIM are complementary approaches: GLMM examined the effect of environmental variables on reptile metrics and species-specific abundances of two lizard species, whereas ANOSIM compared matrices of species abundances between transect classes.

Only two lizard species were found in high numbers to allow specific statistical analyses. Thus, the environmental and fire variables were used to test their effects on the abundance of the two commonest lizard species of the study area, *Psammodromus algirus* and *Podarcis guadarramae*. We first ran GLMM with all the factors, selected the best model according to AIC values using backward selection via "drop1" command, and re-ran the best model with the selected environmental and fire variables to examine the significance effect on lizard abundances.

At the micro-habitat scale, we used geo-referenced reptile locations to test the effects of plant richness and vegetation cover (tree, shrub, and herbaceous cover) at each 20-m section on the probability of reptile presence, reptile abundance, and reptile richness. For this, we used GLMM with "Transect" as the random effect, and binomial distribution (for probability of reptile presence) or Poisson distribution (for reptile abundance and species richness).

All the analyses were performed using the R software packages ggplot2, car, MuMIn, gamm4, and lme4 (R Development Core Team, 2015).

3. Results

In total, we observed 433 reptiles belonging to 14 species (70% of the total species occurring in the Natural Park; see Supplementary Materials Table S2). The ground-dwelling lizard *Psammodromus algirus* was the most abundant species representing 83% of all sightings and was detected in all transects. The second most common species was the wall lizard *Podarcis guadarramae*, representing ca. 6% of the sightings and detected in 55% of surveyed transects.

At the landscape scale, vegetation heterogeneity and plant richness positively influenced reptile abundance and evenness (Table 1; Fig. 1). Likewise, reptile abundance differed among land-use types, as natural woodlands had the highest abundance whereas monocultures showed the lowest abundance (GLMM with "Visit" as random effect; $F_{2,14} = 3.76$, $P = 0.05$; Fig. 2). Reptile evenness declined with time since fire, while fire recurrence had no significant effect on any of the reptile metrics (Fig. 1). Also, none of the variables considered exerted any effect on species richness (Table 1). Regarding differences in the reptile community composition (species presence and abundance), the

Table 1

Results of the GLMM analysis for three reptile-community metrics: Reptile abundance, Species richness, and Pielou's evenness. Only the results for the best model selected are presented.

	Reptile abundance			Species richness			Pielou's evenness		
	Estimate	*Z* value	*P*	Estimate	*Z* value	*P*	Estimate	*t* value	*P*
Fire recurrence		n.s.			n.s.			n.s.	
Time since fire		n.s.			n.s.		−0.01	−2.25	0.020
Vegetation heterogeneity	1.13	1.89	0.060		n.s.		−1.16	−2.03	0.040
Plant richness	0.06	2.64	0.008		n.s.			n.s.	
Land use type		n.s.			n.s.			n.s.	
Land-use diversity		n.s.			n.s.		0.51	1.60	n.s.

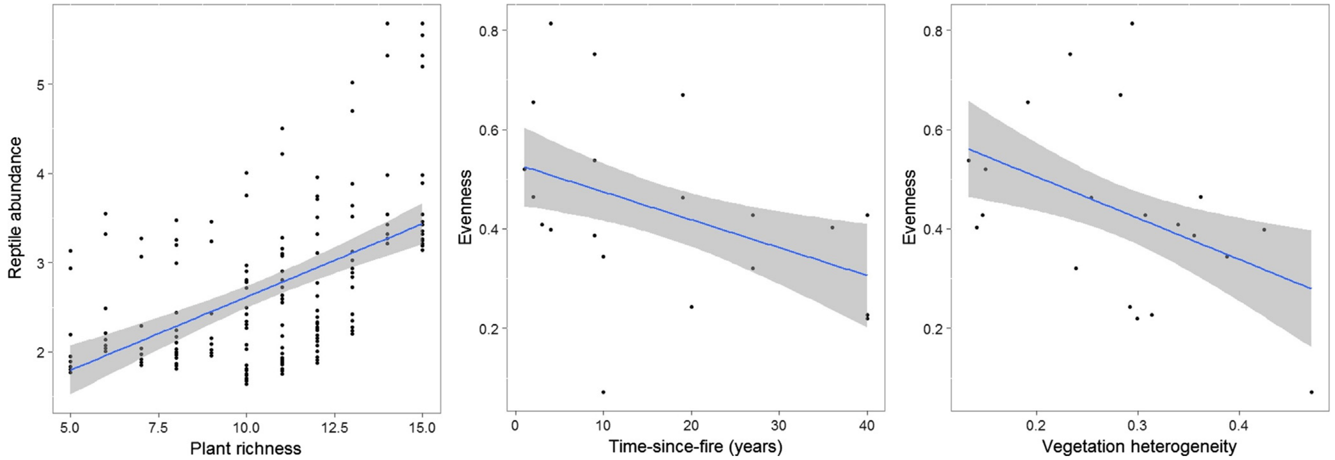

Fig. 1. Significant Generalized Linear Mixed Models' association between reptile metrics (abundance and evenness) and predictive variables plant richness, time-since-fire and vegetation heterogeneity) at Serra de Estrela Natural Park.

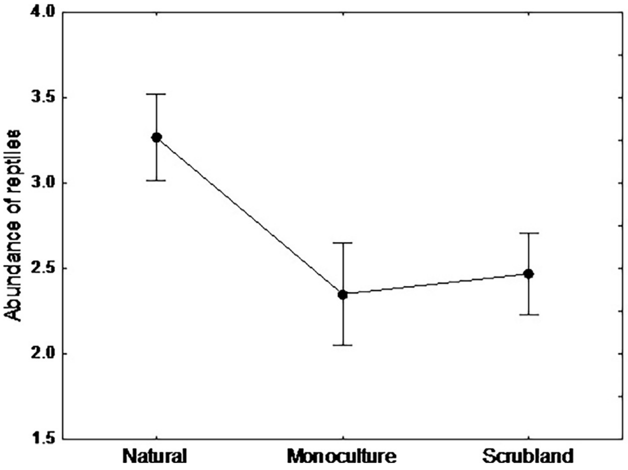

Fig. 2. Mean and standard error scores of the reptile abundance per transect in relation to land-use type.

ANOSIM showed differences between the three land-use types (R = 0.155, $P = 0.044$), especially between natural and scrubland transects ((R = 0.22, $P = 0.036$). Differences were also observed according to time-since-fire intervals (R = 0.227, $P = 0.013$), especially between recently and medium-burnt transects (R = 0.445, $P = 0.007$).

The abundance of *P. algirus* was positively affected by both vegetation heterogeneity and the plant richness in the transects, whereas time since fire and fire recurrence did not significantly affect its abundance (Table 2; Fig. 3). The abundance of *P. guadarramae* was affected by fire recurrence (positive effect) and the time since fire (negative effect; Table 2); that is, this lizard was more abundant in open habitats as those produced by recurrent and recent fires. Moreover, *P. guadarramae* was negatively affected by vegetation heterogeneity and positively affected by plant richness (Table 2; Fig. 3).

Table 2
Results of the GLMM analysis for the abundance of *Psammodromus algirus* and *Podarcis guadarramae*. Only results for the best model selected are presented.

	P. algirus abundance			*P. guadarramae* abundance		
	Estimate	*Z* value	*P*	Estimate	*Z* value	*P*
Fire recurrence		n.s.		0.49	2.10	0.04
Time since fire		n.s.		−0.06	−2.61	0.009
Vegetation heterogeneity	1.94	3.09	0.002	−6.55	−2.55	0.010
Plant richness	0.06	2.71	0.007	0.42	2.61	0.009
Land-use type		n.s.			n.s.	
Land-use diversity		n.s.			n.s.	

At the micro-habitat scale, both the probability of reptile occurrence, reptile abundance and species richness were positively related to plant richness and negatively related to tree cover (Table 3; Fig. 4), suggesting a major effect of the micro-habitat on reptiles.

4. Discussion

This study combined the use of variables at the landscape and micro-habitat scales to understand the response of a Mediterranean reptile community in a fire-prone region of the Iberian Peninsula. We acknowledge that the sampling methodology and effort were not enough for keeping adequate data for a complete view of the overall reptile community response to fire. In our study area, many species (especially snakes) are rare and difficult to detect. However, our results are reasonably adequate for common lizard species (see similar conclusions in Australian Banksia woodlands, Hu et al., 2016).

Despite the fire history of the study area, fire frequency and time since fire only partially explained the reptile species community metrics. Specifically, reptile evenness decreased with the time since fire. However, species-specific analyses demonstrated opposing responses between lizard species. This result suggests that Mediterranean reptiles can present diverse and complex responses to fire (see also similar conclusions in Pastro et al., 2013) that can be masked by the relevance of habitat factors, and corroborates the sensitivity of reptiles to changes in habitat complexity (Santos et al., 2016). Additional variables such as fire return interval, percentage of burned area and fire intensity/severity should be included in future modeling efforts.

4.1. Community-metric results

Most of the reptiles observed in our study were Mediterranean lizard species (Sillero et al., 2009). These lizards typically prefer open habitats (Ferreira et al., 2017) in part due to their physiological capacity to reduce water loss (Ferreira et al., 2016a). Accordingly, we could expect positive responses at recently burnt habitats as previously observed in other regions (Driscoll and Henderson, 2008; Ashton and Knipps, 2011; Driscoll et al., 2012). In our study, reptile (primarily lizards) abundance was strongly related to habitat quality both in terms of the heterogeneity and plant richness (Fischer et al., 2004; Pastro et al., 2013), as well as land-use type. This result confirms that non-natural land uses, with low plant diversity, such as monocultures can be inadequate for Mediterranean reptiles (Azor et al., 2015) most likely due to their low thermal quality (Schreuder and Clusella-Trullas, 2016).

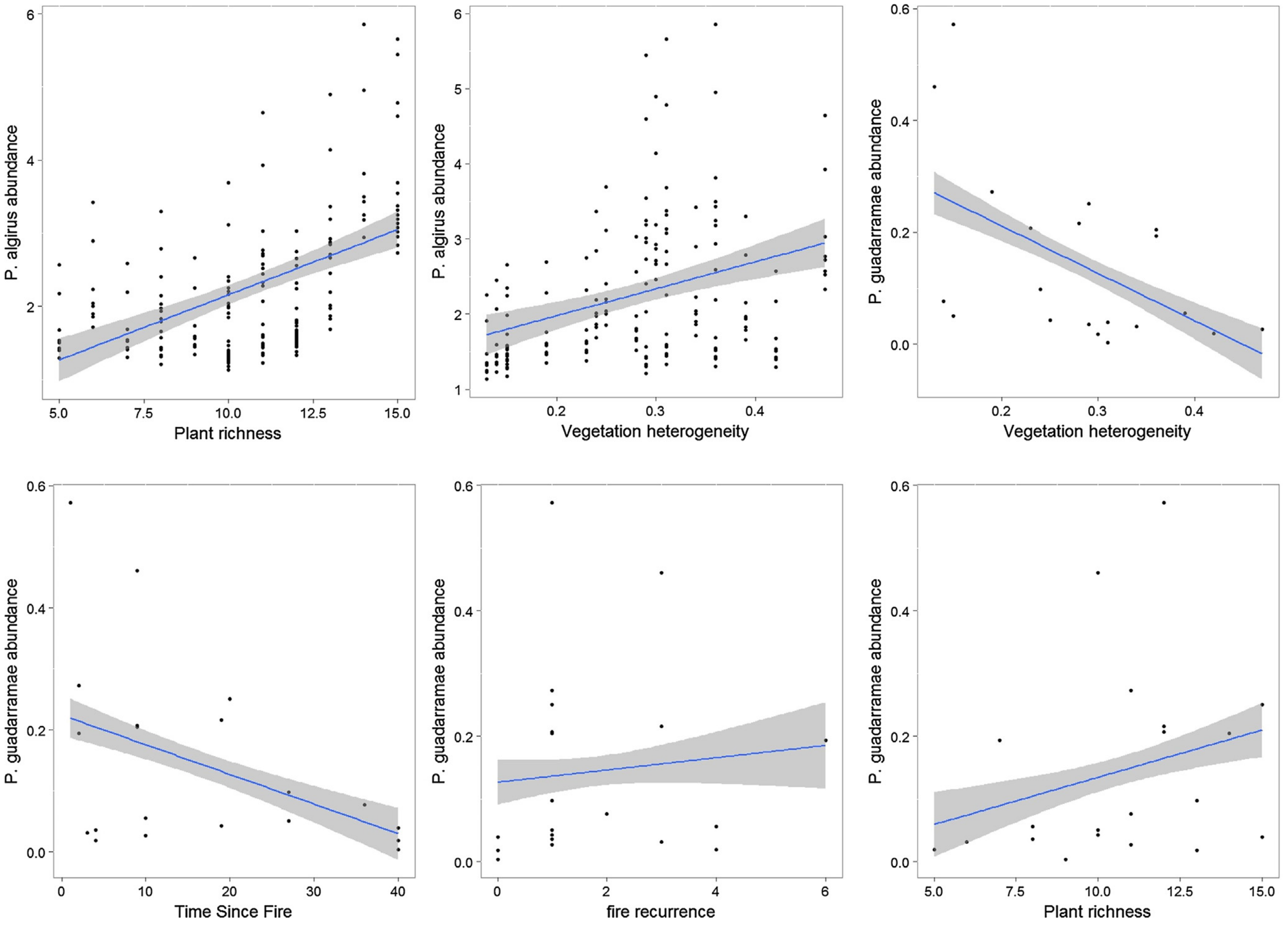

Fig. 3. Significant Generalized Linear Mixed Models' association between *P. algirus* and *P. guadarramae* abundances and plant richness, vegetation heterogeneity, time since fire, fire recurrence, and plant-richness predictive variables at Serra de Estrela Natural Park.

Thus, the strong effect of land use (e.g., pine plantation) can be masking fire effects. Accordingly, in regions dominated by monocultures, land use can be a stronger driver of reptile abundance/community composition than fire history.

Surprisingly, none of the variables studied turned out to affect reptile richness. This may be due to species replacement between transects of different fire histories (Santos et al., 2016), or because the analysis was confounded by the overall low species richness on transects. We acknowledge that other sampling methods such as drift fences might be less biased towards a few abundant lizard species. However, the active searching was effective in other Mediterranean areas giving good results in terms of species richness and diversity (e. g. Santos and Cheylan, 2013).

We found a significant association between reptile evenness, fire history (time since fire) and habitat (vegetation heterogeneity) variables, as long-unburnt sites held less complex reptile communities (lower evenness) than did recently burnt ones. This result contrast with other studies showing that long-unburnt natural woodlands had more diverse and rich reptile communities than burnt sites (Santos and Cheylan, 2013; Ferreira et al., 2016b). In our study area (SENP), long-unburnt sites were often monocultures with a dense canopy and low understory that held a low reptile diversity. This exemplifies the importance of the interaction effect of fire history and land use to understand the reptile responses to fire in highly human-modified landscapes such as the Mediterranean basin.

4.2. Micro-habitat scale effects on community metrics

The micro-habitat scale (i.e. habitat characteristics at the location where reptiles were observed within the transect, at each 20 m section) more clearly explained the patterns of reptile occurrence, than the analysis at broader scale, a pattern demonstrated in previous studies

Table 3
Results of the GLMM analysis for the Probability of reptile presence, reptile abundance and species richness in relation to vegetation cover (tree, scrub and herb) and plant richness. Only results for the best model selected are presented.

	Reptile presence			Reptile abundance			Species richness		
	Estimate	*Z* value	*P*	Estimate	*Z* value	*P*	Estimate	*Z* value	*P*
Tree cover	−0.48	−1.82	0.07		n.s.		−0.29	−1.72	0.09
Scrub cover		n.s.			n.s.			n.s.	
Herb cover	−0.54	−1.84	0.07		n.s.			n.s.	
Plant richness	0.12	2.55	0.01	0.06	2.21	0.03	0.07	2.57	0.01

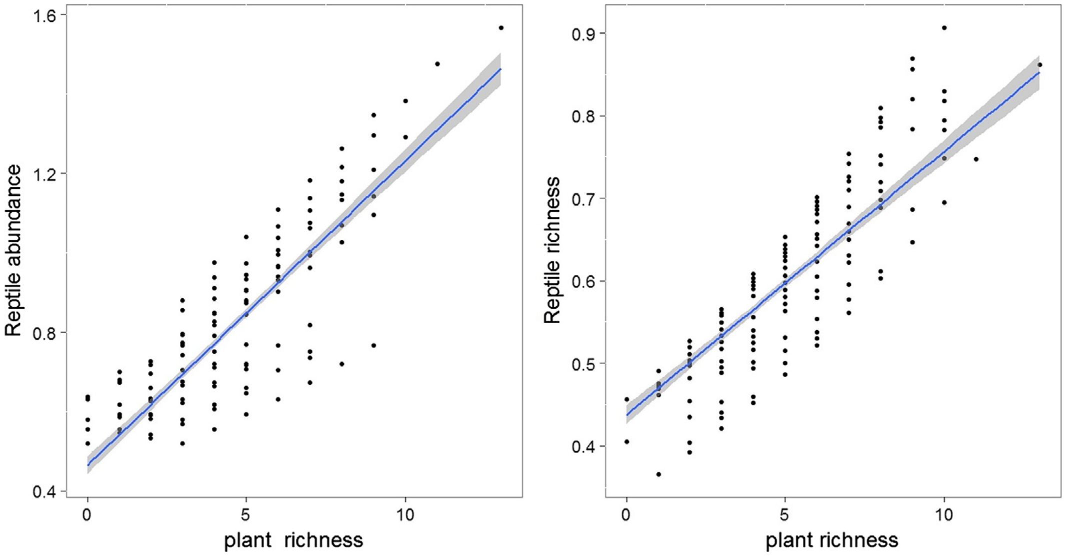

Fig. 4. Relationship between plant richness and reptile abundance (a), and reptile richness (b) at the micro-habitat scale.

(Driscoll and Henderson, 2008; Santos and Poquet, 2010). Our results showed that the probability of reptile presence increased with the richness of plant species. A similar result was observed for reptile abundance at the landscape scale and confirmed that reptile community patterns in response to environmental disturbance can operate at different scales (Ferreira et al., 2017). In parallel to the importance of solar radiation for reptile thermoregulation (Webb and Shine, 2008; Schreuder and Clusella-Trullas, 2016), the presence of different plant species can offer different niches for reptiles and can increase food provision (herbaceous plants and scrubs attract many pollinators; Potts et al. 2003), shelter, and protection against predators (Santos et al., 2016).

Contrary to plant richness, tree cover had a negative effect on all the reptile community metrics (Ferreira et al., 2017). Other studies have also demonstrated a strong connection between thermal properties of the habitat and reptile habitat selection in the Mediterranean (Ferreira et al., 2017) and elsewhere (Martín and Salvador, 1995; Meik et al., 2002), and finally reptile performance (Sears and Angilletta, 2015). Our study indicates that these environmental properties at the micro-habitat scale are relevant to understand the occurrence patterns of reptiles in fire-prone regions.

4.3. Species-specific responses: P. algirus and P. guadarramae abundance

Psammodromus algirus responded positively to the habitat heterogeneity, increasing its abundance while the habitat increased its complexity. This lizard is a ground-dwelling specialist and habitat generalist (Carrascal and Díaz, 1989; Salvador, 2015). It is able to successfully adapt to areas affected by fire (Santos and Poquet, 2010) and it is also common in long-unburnt transects, both in natural woodlands and in monocultures (this study).

Contrary to *P. algirus*, the abundance of *Podarcis guadarramae* was driven by a number of variables, and confirmed its habitat specialization in rocky spots (Diego-Rasilla and Perez-Mellado, 2003). The extreme structural changes caused by recurrent (or recent) fires provided conditions (open rocky spots) that favored this wall lizard (Ferreira et al., 2016b, 2018). Thus, habitat specialization merits consideration in evaluating the effects of fire on reptiles (Hu et al., 2016; Santos et al., 2016).

4.4. Conservation remarks

The study site has been historically affected by fires, and fire frequency, intensity and extent have increased remarkably in recent years. However, we found that fire history factor (particularly fire recurrence) had little impact on the reptile communities. Indeed, the rock lizard *P. guadarramae* was more abundant in open habitats produced by recurrent and recent fires. On the contrary, habitat characteristics such as vegetation complexity (positive effect) and land transformation to monocultures (negative effect) were likely important drivers of reptile occurrence in fire-prone areas. Monocultures have long been a source of economic income in SENP as well as in many other areas of northern Portugal. However, monocultures are inadequate habitat for Mediterranean reptiles (Azor et al., 2015), and if they replace late successional (mature) habitats, local extinctions of some reptile species can occur (Driscoll et al., 2012; Valentine et al., 2012). The SENP region supports the highest herpetofaunal biodiversity in Portugal (only paralleled by Peneda-Gerês National Park) and thus, should be a national priority for the conservation of the reptile biodiversity. The development of management programs to promote pyrodiversity could be an adequate practice to enhance reptile diversity, as previously observed in other vertebrate taxa (Tingley et al., 2016; Kelly and Brotons, 2017).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.03.029.

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