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Responses of reptiles to fire in transition zones are mediated by bioregion affinity of species

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Abstract Fire has impact on reptile communities with marked shifts in community composition between burnt and unburnt areas. These shifts are often related to the preference of reptile species throughout early or late post-fire successional habitats. Areas located in transition zones between bioregions harbor complex reptile communities with a mixture of biogeographic affinities. In these biogeographic crossroads, since fire simplifies the habitat structure, we expected simpler (lower alpha diversity) and more similar (lower beta diversity) reptile communities within burnt than within unburnt localities. We have tested this hypothesis in a transition zone between the Atlantic and Mediterranean bioregions in northern Portugal. Reptiles were surveyed in five localities (8 times per locality) along fire edges in which each locality was composed of one burnt and one unburnt transect. In total, 588 reptiles from 10 species were recorded. Unburnt transects had higher alpha and beta diversity and higher relative abundance of non-Mediterranean individuals than did burnt transects. A redundancy analysis also showed contrasting responses of Mediterranean and non-Mediterranean species, the former increasing and the latter decreasing after fire. Our study demonstrates that fire reduced the complexity of the reptile community, with benefits towards Mediterranean species due to its environmental preferences and long evolutionary association to fire. In biogeographic crossroads such as the

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study area, the retention of long unburnt vegetation is expected to maintain more diverse reptile communities.

Keywords Biogeographic transition · Functional responses · Mediterranean · Reptiles · Wildfire

Introduction

Fire is a common disturbance in many ecosystems around the world (Bond et al. 2005; Moritz et al. 2012; Spies et al. 2012) with profound effects on diversity and composition of plant and animal communities on large spatial and temporal scales (e.g. Pausas and Verdú 2008; Nimmo et al. 2014; Driscoll et al. 2010; Pastro et al. 2014). In the Mediterranean basin, one of the world's biodiversity hotspots (Myers et al. 2000), fire is among the most important natural disturbances (Keeley et al. 2012). Mediterranean landscapes are, therefore, dominated by fire-prone ecosystems with vegetation resulting from a long evolutionary association with fire (Pausas and Keeley 2009). In recent decades, fire frequency and extension is increasing in the Mediterranean basin (Pausas and Fernández-Muñoz 2012) due to synergic effects of land abandonment and global warming (Piñol et al. 1998; Moreira et al. 2001; Pausas 2004). Given these processes, studying the species' response to fire becomes a conservation priority.

Many studies in Mediterranean ecosystems have linked animal-community responses to fire with the post-fire changes in vegetation composition and structure (e.g. Torre and Díaz 2004; Sarà et al. 2006; Vallecillo et al. 2008; Santos and Cheylan 2013). In the short term, fire induces fundamental alterations in habitat structure (Grant et al. 2010; Hu et al. 2013), e.g. canopy simplification, and local environmental conditions such as higher incoming solar radiation (Russell et al. 1999; Haslem et al. 2011). Fire opens the habitat but also increases scrubland diversity, benefiting animals adapted to these post-fire conditions (Bury 2004; Brotons et al. 2008; Santos and Poquet 2010). Over post-fire succession, vegetation evolves to the pre-fire situation. Fox (1982) predicted that in parallel to changes in vegetation, animal communities can also shift following the habitat-accommodation model of succession.

Reptiles, being ectotherm organisms, are sensible to habitat structure and modification (Pianka 1989; Driscoll et al. 2012) due to their thermal constraints and specialization (Huey 1982). At larger scales, their range distribution is greatly influenced by climate and specifically by temperature (Aragón et al. 2010). Accordingly, reptiles show strong responses to fire (e.g. Letnic et al. 2004; Santos and Poquet 2010; Nimmo et al. 2012; Valentine et al. 2012). A number of field-based reptile studies found no support for the habitat-accommodation model (Driscoll and Henderson 2008; Lindenmayer et al. 2008; Driscoll et al. 2012; Nimmo et al. 2012; Hu et al. 2013). However, most of them reported that relative abundance of many species varies according to time since fire (Nimmo et al. 2012; Smith et al. 2013; Kelly et al. 2015), implying that some species tend to prefer early, middle or late successional vegetation (Valentine et al. 2012; Davis and Doherti 2015; Kelly et al. 2015; Santos et al. 2015). The lack of overall support for predictions of Fox's model (1982) has been reported for other groups such as small mammals and birds (Kelly et al. 2011, 2015), although again some species within a community respond to long-unburnt or recently burnt habitats.

In this study, we examine responses of reptiles to fire at a biogeographic crossroads. These areas are characterized by a mixture of species with different biogeographic affinities (Spector 2002). In these scenarios, species can occur in sympatry with subtle segregation in microhabitat use (Pianka 1973), or differences in thermal or activity preferences (Langklide and Shine 2004) according to their biogeographic affinities. Thus, in complex communities such as those located in transition zones between bioregions, we hypothesize that responses to fire can be mediated by the biogeographic affinity of species as well as their distinctness in terms of microhabitat selection (Ferreira et al. 2016). In other words, our aim was to identify whether species that have the highest probability of occurrence in burnt and unburnt sites are correlated to their biogeographic affinity.

We examined this general hypothesis at the Peneda-Gêres National Park (northern Portugal), a protected area located near to the transition zone between Atlantic and Mediterranean bioregions and affected by frequent fires. Although at a large scale it is included in the Atlantic bioregion (EEA 2011), it brings together species with both biogeographic affinities. This bioregion transition results in a mixed reptile community (Soares et al. 2005; Soares and Brito 2007), providing an opportunity to test which fire successional vegetation reached more diverse communities. In the Mediterranean region, crown fires simplify the habitat structure mainly by eliminating the tree *strata* (Keeley et al. 2012). Greater post-fire incoming solar radiation is expected to benefit Mediterranean species, as previously reported in other Mediterranean reptile communities exposed to thinning management in conifer plantations (Azor et al. 2015).

At long unburnt sites, the vegetation tends to return to more complex pre-fire successional stages; this complexity is expected to support more complex reptile communities, i.e. Mediterranean and non-Mediterranean species, with segregation niches between species co-occurring in sympatry (Luiselli 2006; Žagar et al. 2013). Late successional vegetation provides suitable microhabitats for a range of animals from early to late vegetation stages; the contrary rarely occurs (Kelly et al. 2015; but see Torre and Díaz 2004). Thus, we expect to identify more similar reptile communities in recently burnt (less complex) habitats, this is lower beta diversity values, and more diversified and heterogeneous communities (i.e. higher beta diversity values) in long unburnt areas, as documented previously in other Mediterranean localities (Santos and Cheylan 2013).

The objective of this study was to survey reptiles in recently burnt and unburnt transects located in a transition zone between two bioregions, and to compare community metrics (species richness and diversity) and relative abundance of Mediterranean and non-Mediterranean reptiles between them. The specific questions addressed were: (i) Due to the differential responses to habitat between Mediterranean and non-Mediterranean species (Sillero et al. 2009), does the reptile community in unburnt to burnt sites differ according to specific bioregion affinities of species? (ii) Is the reptile community less diverse in burnt compared to unburnt sites? (iii) Given the short-term simplification of the habitat after fire, did reptile assemblages become more similar among burnt than among unburnt sites?

Materials and methods

Study area

Our study area is located in the Peneda-Gêres National Park (PNPG), in the north-western Iberian Peninsula (Fig. 1). Its altitude varies from 140 to 1545 m a.s.l. with mean air

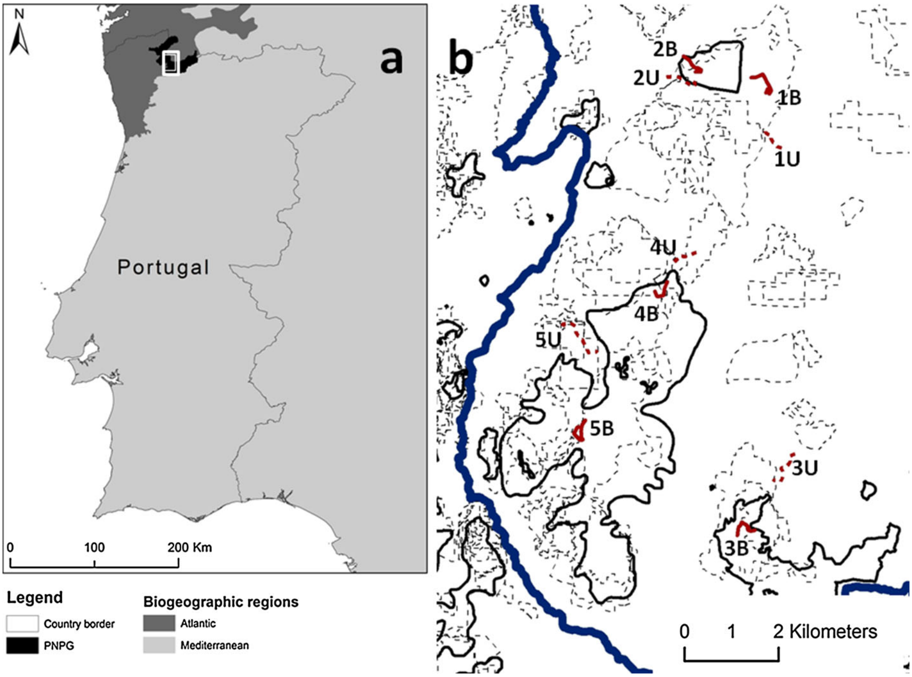


Fig. 1 **a** Location of the Peneda-Geres National Park (PNPG) and boundaries of Mediterranean and Atlantic bioregions. **b** Spatial scheme of the five pairs of transects, four of them located on edges of recent fires (2010 and 2012, *solid-line black polygons*), and one of them on the edge of an old fire (before 2010, *dashed-line black polygons*). *Wide solid line*: limit of the PGNP. Transect symbols: (U) unburnt transects; (B) burnt transects. Sites: Albergaria (1), Barragem (2), Ermida (3), Mirador (4), Near Mirador (5)

temperature of 7.9 °C in January to 20.3 °C in July. Its high levels of precipitation give a mean annual rainfall of 3200 mm, with maximum values in winter and spring, and minimum values during the summer (Vieira 1996).

Due to its location, PNPG is close to the transition between the Mediterranean and Atlantic bioregions, and consequently has remarkable climatic diversity, resulting in a high natural value that holds a diverse array of flora, fauna, landscapes, and ecosystem types (Honrado et al. 2001), where typical Atlantic and Mediterranean species co-exist in the same area (Soares et al. 2005; Araújo et al. 2006). Deciduous oak forests of *Quercus robur* alone or mixed with *Q. pyrenaica*, and mixed deciduous and coniferous forests occupy Atlantic areas, whereas *Q. suber* occupies the Mediterranean climatic spots (Honrado et al. 2001). Major shrubs include *Erica* sp., *Ulex* sp., and *Cytisus* sp. (Serra and Carvalho 1989). *Eucalyptus* plantations and invasive *Acacia* sp. trees are also frequent in some areas of the park.

The PNPG is one of the richest herpetological areas in Portugal (Loureiro et al. 2008) with 20 reptile species registered (Soares et al. 2005; Soares and Brito 2007) with a combination of Atlantic and Mediterranean species, reflecting its location near to the Mediterranean-Atlantic transition. We classified all reptiles in our study as Mediterranean or non-Mediterranean species following Sillero et al. (2009) although with some differences (Supplementary Materials Table S1). A weak point in the Sillero et al. (2009) paper is that they did not model species including complete distributions, and admitted that with a complete distribution approach, it would have been possible to detail chorotypes and to cluster Iberian endemic species separately from European or Palearctic ones (e.g. *Natrix natrix*). This point has been solved in the New Atlas of Amphibians and Reptiles of Europe (Sillero et al. 2014). According to the whole distribution, particular habitat preferences, and ecological requirements, we do not consider certain Palearctic species of wide distribution in Europe to be Mediterranean species.

The PGNP is frequently affected by fires likely caused by humans (Catry et al. 2009). The Instituto de Conservação da Natureza e das Florestas (ICNF; http://www.icnf.pt/portal/florestas/dfci/inc/info-geo) reported for the period 1975–2009 that 52.3 % of the Park extent has been burnt at least once. The recurrence of fire is high, with 23 % of the area having undergone at least two fires and 2 % having been burnt more than five times in the same period.

Sampling design and reptile fieldwork

In spring-summer 2012–2014, we sampled reptiles at five sites located on fire edges within the PNPG (the fire history of each site was retrieved from the ICNF database). Four of these sites were affected by recent fires (i.e. 2010 or 2012, Supplementary Materials Table S2). At each site, we selected two transects, one located on the burnt and the other on the unburnt side of fire edges (Fig. 1), and compared reptile abundance in these pairs of transects. Sites and transects were selected according to the following criteria: (1) each pair of transects belonged to the same fire event; (2) transects were located on unpaved trails in order to maximize reptile detectability usually associated with open points (see a similar methodology in Santos and Cheylan 2013), and therefore, at some sites both transects are quite far apart; (3) each pair of transects was located as close as possible (average distance between pairs 698 m; see details in Supplementary Materials Table S2); and (4) the starting point of transects was set at more than 100 m from the limits of the fire to avoid ecotone effects on reptile counts with a potential mixture of species adapted to unburnt and burnt habitats. Transects averaged 715 m in length (see details in Supplementary Materials Table S2) and were located at an average of 769 m altitude.

Each transect was visited 8 times by one researcher with uniform time-constrained effort of 45 min per visit, resulting in a total of 80 visits. All transects were visited each year and pairs of transects were visited at the same time (one transect of each pair by one of the researchers) to avoid biases on reptile abundances due to climatic conditions. Surveys were made with favorable weather conditions in order to maximize reptile activity and detectability. In transects, reptiles were found by visual surveys and additionally by searching potential spots or shelters. The reptiles sighted were identified to the species level. Recently burnt sites are often less vegetated areas than unburnt ones, and hence it might result in higher reptile detectability. However, the sampling methodology here applied has been previously used in southern France; in that locality, the distance at which each individual was detected from the line of the transect did not vary within each species between burnt and unburnt transects (Santos and Cheylan 2013). The potential detectability bias between burnt and unburnt transects would be solved by the fact that transects were conducted on trails, shelters were also examined, and some reptiles were detected by the noise produced on the vegetation when escaped from the researcher proximity.

Additionally, habitat structure of transects was characterized by recording the abundance of four habitat types (i.e. bare ground and rocks, scrubland, open forest, and dense forest) along the reptile transect by Google Earth Imagery in 2013. Habitat types were recorded at points 25 m apart along transects. We constructed a matrix of habitat-type relative abundances that was transformed to the percentage of each habitat type at each transect. Finally, percentages were arc-sin transformed for further statistical analyses.

Data analysis

We calculated the pair-wise correlation of fire-history (time since fire and number of fires) and habitat-structure (abundance of each habitat type) variables. This preliminary analysis was aimed at determining whether fire drives habitat changes, and therefore the potential effect of both types of variables, fire history and habitat structure, can represent the same phenomenon. Pair-wise correlations were calculated with parametric Spearman tests after rank transform fire-history variables to achieve normality (Shapiro–Wilk's W test $p > 0.05$).

Due to the low detectability of many reptile species, the reptile community at each transect (species richness and specific abundances) was characterized by adding together abundance values recorded for the eight visits. Thus, each transect was treated as an individual unit for analyses. We created a matrix of relative abundances of reptile species per transect. For each transect, we calculated four community metrics: total number of reptiles, species richness, Simpson's diversity (alpha diversity) and Pielou's evenness, as well as relative abundance of Mediterranean and non-Mediterranean reptiles.

At each site, transects were categorized as burnt and unburnt within each pair. We acknowledge that the burnt transects in Albergaria had been affected only by an old fire that occurred in 1989 whereas the unburnt transect in Near Mirador had been affected by fires in 2006 and partially in 2007 (Supplementary Materials Table S2). Thus, burnt transects in some sites were similar to unburnt transects of other sites in terms of fire history. However, our design and further pair-wise analyses examined differences within each pair, hence considering the non-independence of each pair. Although the burnt transect in Albergaria was affected only by one old fire in 1989 (Supplementary Materials Table S2), a close inspection of the vegetation suggested that a more recent fire occurred at this site although it was not registered in the ICNF data base.

Due to the sampling design, differences between burnt and unburnt transects in community metrics were compared by Wilcoxon Matched-Pairs test, a nonparametric test that compares two paired groups. This method did not take into account the fire history (time since last fire and number of fires) of each transect; however, since each pair is not independent, and due to the low number of transects sampled ($N = 10$) we considered it inappropriate to examine the effect of fire history on reptiles by General Additive Models, a method often employed in other studies (e.g. Valentine et al. 2012; Hu et al. 2013; Nimmo et al. 2014; Santos et al. 2015). The Wilcoxon Matched-Pairs test was used to compare differences in reptile-community metrics and the relative abundance of species between each pair of burnt and unburnt transects.

From the overall matrix of relative-abundance data, we calculated the similarity between all pairs of transects with the Bray-Curtis similarity index. This index gives a degree of correspondence (based on presence/absence and abundance of species) between all pairs and corresponds to a measure of beta diversity. Through the resulting matrix of similarity, we performed an ANOSIM test, i.e. a non-parametric analysis to detect differences between groups of transects (i.e. burnt vs. unburnt), which uses permutation/randomization methods on a similarity matrix. We also examined whether reptile communities were more similar among unburnt or among burnt transects comparing Bray-Curtis similarity scores. Similarly, we examined differences in vegetation structure between burnt and unburnt transects with ANOSIM. Statistical analyses were performed whit PRIMER v5 (Clarke and Gorley, 2001) and STATISTICA v10 (Statsoft Inc. 2010).

Multivariate analyses were used to visualize the association between species abundance (classified as Mediterranean and non-Mediterranean) with the burnt and unburnt classification of transects. Firstly, from the matrix of relative abundances, the longest gradient in a Detrended Correspondence Analysis (DCA) was 1.111, indicating a linear distribution of the data. Accordingly, we examined the relationship between variables (reptile abundances) and fire condition (burnt and unburnt) using a redundancy analysis (RDA), and tested the relationship between the axes and variables using a Monte Carlo permutation test (ter Braak and Šmilauer 2002). These multivariate analyses were performed with CANOCO (ter Braak and Šmilauer 2002).

The relative abundance of the three commonest species (*P. guadarramae*, *P. bocagei*, and *P. algirus*) were examined by general linear mixed models (GLMM) using site as random effect, fire condition (burnt and unburnt) as fixed effect, and its interaction as factors. Since these species were common in most transects, we used reptile counts for each visit as independent data. To meet the assumption for normality, residuals of the dependent variable on the grouping factors were examined.

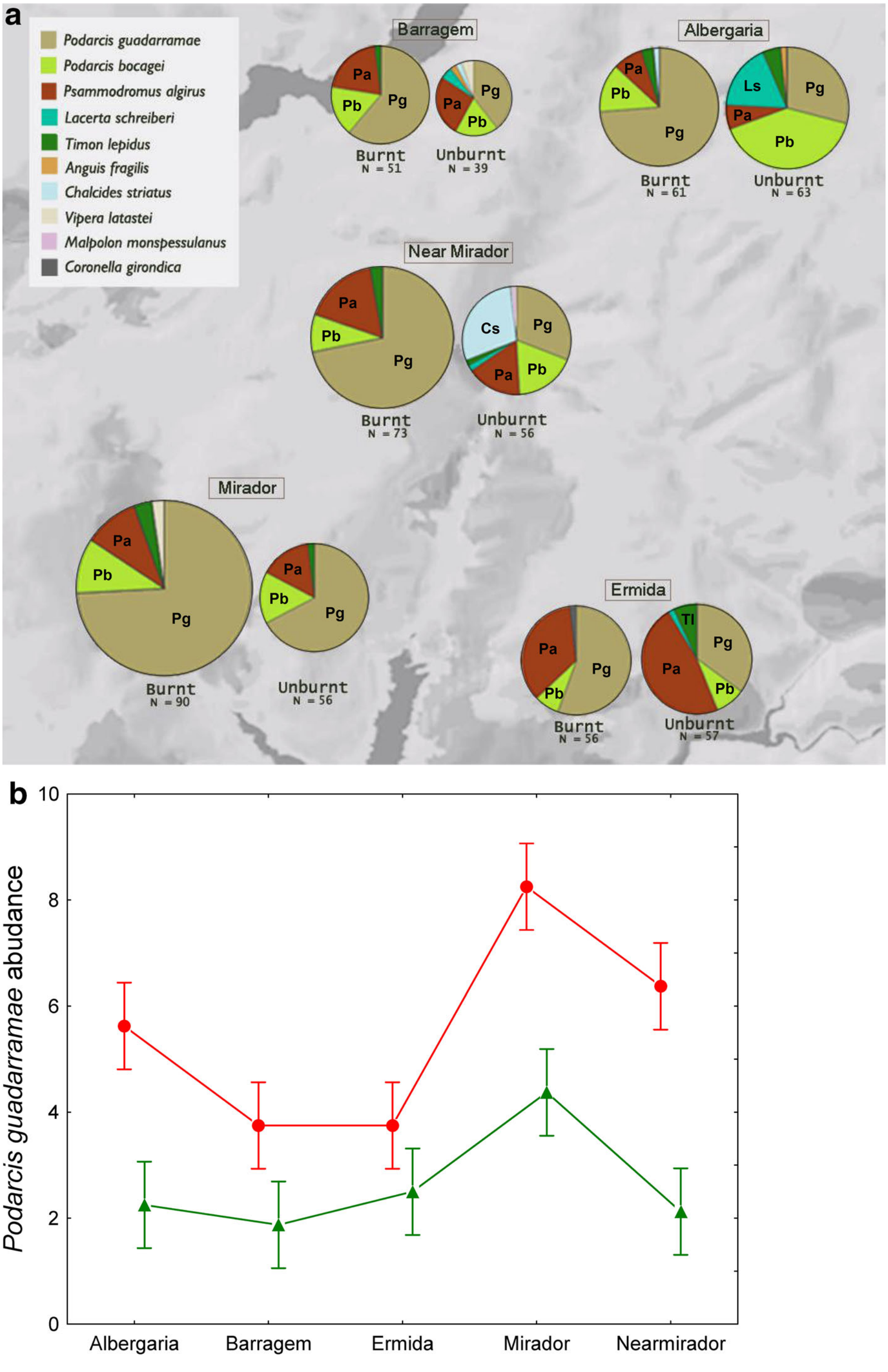
Results

ANOSIM showed that the habitat structure differed between burnt and unburnt transects ($R = 0.436$; $P = 0.04$). Pair-wise correlations of fire-history variables with habitat-structure variables showed that transects with high values for time since fire and low values of number of fires had denser canopy (i.e. dense forest) extent (Supplementary Materials Table S3). Apparently, the extent of other habitat-structure variables was not related to the fire-history variables.

We recorded 588 individual reptiles from 10 species (Supplementary Materials Table S4), including 5 lizards, one anguid, one skink, and three snakes (one viper and two colubrid species). The abundance of three species (*Podarcis guadarramae, Podarcis bocagei*, and *Psammodromus algirus)* represented 90 % of the total number of individuals found. *Podarcis guadarramae* itself represented 56 % of the observations (Fig. 2a). The species richness or the total number of reptiles seen did not show significant differences between unburnt and burnt transects (Wilcoxon Matched-Pairs tests; $Z = 1.48$, $P = 0.14$; and $Z = 1.21$, $P = 0.22$ respectively), although the first metric was higher in the unburnt transect in 4 out of 5 pairs. Unburnt transects had higher Simpson's diversity (alpha diversity) and Pielou's evenness scores than their burnt pairs (both analyses $Z = 2.02$, $P = 0.04$). The relative abundance of Mediterranean reptiles was higher in all burnt transects compared to their unburnt pairs ($Z = 2.02$, $P = 0.04$); the opposing pattern was of course found for non-Mediterranean reptiles.

ANOSIM showed that the reptile community differed between burnt and unburnt transects ($R = 0.36$; $P = 0.02$). Moreover, the Bray-Curtis similarity scores were higher in the comparison between pairs of burnt transects than between pairs of unburnt transects ($t = 4.71$, df $= 18$, $P = 0.0002$). This result indicates that the beta diversity was higher among unburnt sites than among burnt ones.

GLMMs for the three commonest species showed opposing results. The relative abundance of the Mediterranean lizard *P. guadarramae* proved higher in burnt transects ($F_{1,70} = 25.28$, $P = 0.007$), a tendency to differ among sites ($F_{4,70} = 4.46$, $P = 0.09$)


a
Podarcis guadarramae
Podarcis bocagei
Psammodromus algirus
Lacerta schreiberi
Timon lepidus
Anguis fragilis
Chalcides striatus
Vipera latastei
Malpolon monspessulanus
Coronella girondica
Barragem
Burnt N = 51
Unburnt N = 39
Albergaria
Burnt N = 61
Unburnt N = 63
Near Mirador
Burnt N = 73
Unburnt N = 56
Mirador
Burnt N = 90
Unburnt N = 56
Ermida
Burnt N = 56
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◀**Fig. 2** **a** Summary of the relative abundances of reptiles species observed at the ten transects visited after accumulating data of eight visits made at each transect. Acronyms of the commonest species are in pie charts (Pg: *P. guadarramae*; Pb: *P. bocagei*; Pa: *P. algirus*; Ls: *L. schreiberi*, Tl: *T. lepidus*; Ca: *C. striatus*). **b** Relative abundance of *P. guadarramae* on burnt and unburnt transects in the five sites sampled in Peneda-Gerês National Park. *Circles* mean relative abundances of lizards averaged from the eight visits made at each burnt transect; *triangles* mean relative abundances of lizards averaged from the eight visits made at each unburnt transect. *Whiskers* are ± standard errors

with the interaction not being significant (Fig. 2b). This result indicated that, besides fire, other elements that characterize each site (e.g. provision of suitable rocky microhabitat) may influence the relative abundance of this lizard. The Atlantic lizard *P. bocagei* did not show differences on relative abundance between unburnt and burnt transects ($F_{1,70} = 1.40$, $P = 0.4$), although the interaction between burnt/unburnt transects and site was significant ($F = 2.61$, $P = 0.04$); at some sites, the unburnt transect had much more *P. bocagei* than did the burnt, whereas at other sites we found no differences within the pair. Finally, the Mediterranean lizard *P. algirus* showed no differences in relative abundances between unburnt and burnt transects or the interaction, although differences were found between sites ($F_{4,70} = 10.56$, $P = 0.02$).

The RDA confirmed the previous species-specific results with a significant association of species to burnt and unburnt conditions (trace = 0.40, F-ratio = 5.334, $P = 0.002$). Notably, the first axis of this analysis identified *Podarcis bocagei* and *Lacerta schreiberi*, two species of Atlantic non-Mediterranean affinity (Sillero et al. 2009), associated with unburnt habitats (Fig. 3). The latter was found only in unburnt transects with marginal differences according to the Wilcoxon Matched-Pairs test ($Z = 1.83$, $n = 5$, $P = 0.07$). *Podarcis guadarramae*, a Mediterranean lizard, was the only common species associated to burnt areas according to the RDA plot, being more common in burnt transects ($Z = 2.02$, $n = 5$, $P = 0.04$). Finally, three species, *T. lepidus*, *P. algirus*, and *V. latastei* were not clearly associated with any transect according to its fire condition (Fig. 3).

Discussion

Our study demonstrated that the response of reptiles to fire is complex and diverse. Factors such as fire history and severity (Lindenmayer et al. 2008; Driscoll et al. 2012; Hu et al. 2013), prior management practices (Bury 2004; Moreira and Russo 2007), and specific life-

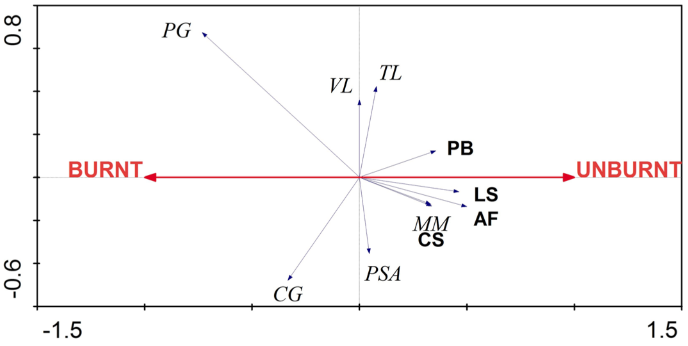

Fig. 3 Redundancy-analysis plot of the association between reptile species and burnt/unburnt condition of the transects sampled in Peneda-Gerês National Park. Abbreviations of species in Supplementary Materials Table S3. Abbreviation types: *Bold* (non-Mediterranean), and *italic* (Mediterranean species)

history traits of species (Driscoll and Henderson 2008; Santos and Cheylan 2013) are important to understand the complexity of reptile responses. Our study adds one factor more, since the reptile-community responses to fire are also driven by biogeographic affinities of species.

Although total reptile abundance and species richness did not vary between burnt and unburnt transects, diversity and evenness were higher in unburnt transects than in their burnt pairs, suggesting more complex and mature communities in unburnt (undisturbed) habitats, as occurred in other Mediterranean localities such as southern France (Santos and Cheylan 2013). Bray–Curtis similarity scores revealed that the five burnt transects studied had more similar reptile assemblages, whereas unburnt areas showed more variation. These results suggest that fire tends to simplify and homogenize reptile communities and reduce beta diversity (Pastro et al. 2011; Santos and Cheylan 2013; but see Farnsworth et al. 2014). This pattern can be mediated by the homogenization of the habitat structure which is shaped by fire (Mouillot et al. 2003), notably by the forest canopy reduction (Santos et al. 2015; this study), which in turn can reduce the diversity of suitable microhabitats for a number of reptile species in transition zones between bioregions.

Our study has demonstrated that the biogeographic affinity (Mediterranean vs. non-Mediterranean) is an important factor that explains the responses of reptiles to fire at biogeographic contact zones. Mediterranean reptile species respond positively to fire probably due to its thermal preferences by open areas (Ferreira et al. 2016) and the long evolutionary association of Mediterranean biota with fire (Pausas and Keeley 2009). In contrast, Atlantic reptile species are more associated with moist environments that are lost by the canopy reduction and habitat simplification. These general trends were also highlighted by the observed opposing species-specific responses to fire within the reptile community. These responses can arguably be explained by particular life-history and functional traits of species (e.g. microhabitat selection, thermal preference, age of sexual maturity, etc.; see for example Santos and Cheylan 2013). In this context, the functional response of reptiles to fire has been associated with the habitat selected by the species (Smith et al. 2013; Santos et al. 2015) or their geographic affinities (Santos and Cheylan 2013). In this work, we found that at least one species increased in burnt areas (*P. guadarramae*) and two displayed negative responses to post-fire environmental conditions (*P. bocagei* and *L. schreiberi*). Unfortunately, for several species (*T. lepidus*, *P. algirus,* and *V. latastei*), it was difficult to fix their responses to fire as a consequence of their likely low population densities. Insufficient data may result in low statistical power, thereby hindering a detectable response to post-fire succession (Driscoll and Henderson 2008; Driscoll et al. 2012).

The Atlantic species *L. schreiberi* responded negatively to fire as it was found only in unburnt transects, and a similar response was found in *P. bocagei*, also an Atlantic species. The link between negative responses to fire and Atlantic affinity can be motivated by species-specific habitat requirements as these species need well-established canopy and moisture to live (Brito et al. 1998; Monasterio et al. 2013). These species, endemic to the Iberian Peninsula and with a range limited to its north-western corner (Sillero et al. 2009), appear to suffer synergic effects related to global warming (Rödder and Schulte 2010). As suggested by Carvalho et al. (2010), climate change might have a serious impact on the distribution patterns of the endemic reptiles of the Iberian Peninsula, particularly for species with Atlantic affinities. These effects, combined with fire-specific responses of Atlantic species could contribute to local extinctions and contraction of their distribution ranges (Gandhi et al. 2001; Woinarsky et al. 2004).

On the other extreme, Mediterranean species such as *P. algirus* showed no clear connection with burnt transects. We argue that its generalized requirements in terms of the habitat (Carretero 2002) allow this lizard to live in a range of burnt and unburnt sites. By contrast, *P. guadarramae*, a Mediterranean species, responded positively to fire. This species usually lives on cliffs and large rocks (Diego-Rasilla and Pérez-Mellado 2003), microhabitats with clearly less impact from fire than that undergone by vegetation. The response of this lizard to fire can be mediated by its association with specific microhabitats, as reported for some Australian reptiles (Driscoll et al. 2012; Davis and Doherti 2015) and other Mediterranean geckos (Santos et al. 2015). The link between fire responses and microhabitat preference can be related to three factors: how much the habitat is affected by fire (i.e. reptiles living on cliffs will respond positively to fire), the frequency of fires (i.e. higher frequency can more severely modify the habitat), and how much time the habitat takes to recover after fire (i.e. species living in leaf litter usually recover slowly; Smith et al. 2013). Moreover, responses of reptiles to post-fire habitat conditions can be linked to their thermal requirements (Pough 1980; Dunham et al. 1989; Huey 1991; Elzer et al. 2013), which in some way can be related to differences displayed by Mediterranean and non-Mediterranean species. However, habitat *per se* may not have a linear response to fire, as a range of location-specific factors such as soil, microclimate, and vegetation composition may drive this response (Driscoll and Henderson 2008; Pastro et al. 2013; Nimmo et al. 2014). Reptiles preferably occupy sites where temperatures, shelter, and food resources become suitable and leave when conditions become unsuitable (Connell and Slayter, 1977; Fox 1982; Masters 1996) and thus previous conditions of each location could influence previous reptiles' distribution. This can be inferred from Fig. 2b, as the parallelism of relative abundances of *P. guadarramae* between burnt and unburnt transects throughout the five different sites probably indicates that, besides fire, other elements characterizing each site (e.g. provision of suitable rocky microhabitat) may influence this lizard's relative abundance, although amplified after the fire.

Conservation remarks

Our study demonstrates that fire reduced the complexity of the reptile community. We found a diversified range of responses to fire, with biogeographic affinities (Mediterranean and non- Mediterranean) being a key driver of these responses. Differences in the reptile community between burnt and unburnt sites according to biogeographic affinities of species mirror differences found elsewhere between early and late successional reptiles (Valentine et al. 2012). Biogeographic crossroads are priority areas for biodiversity conservation (Spector 2002). In the PNPG, a transition zone between two bioregions, repeated fire regimes clearly decrease reptile diversity with negative effects particularly on Atlantic late-successional organisms. Thus, the retention of long unburnt vegetation is likely to have wildlife benefits, maintaining a measure of precaution given the time required to recover such vegetation (Haslem et al. 2011; Nimmo et al. 2012). However, in a scenario where vegetation structure, function, and natural responses have been impaired or negatively altered by anthropogenic activities, the recovery of ecosystems from the effects of fire is likely to be slow, sporadic, and incomplete (Bury 2004) and therefore late successional habitats may be dramatically reduced, resulting in local extinction of late colonizers (Valentine et al. 2012).

Developing management practices that conserve biodiversity in the face of recent altered fire regimes is now critical (Driscoll et al. 2010; Fattorini 2010; Pons and Clavero 2010). Peneda-Gerês National Park should be a priority for the conservation of reptiles at a national scale, especially long-unburnt areas with high reptile diversity due to a mixture of Mediterranean and non-Mediterranean species. It is necessary to adjust fire-management biodiversity conservation to the complex capabilities of species responses to fire, which, once species-specific, need to be coupled with the knowledge of the physiology, behaviour, and historical biogeography of each one, and integrated with management of other processes (e.g. grazing, logging, predator control; Letnic and Dickman 2005). These interactions are important topics for future research.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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