

# Contrasts in short- and long-term responses of Mediterranean reptile species to fire and habitat structure

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**Abstract** Changes in habitat structure constitute a major factor explaining responses of reptiles to fire. However, few studies have examined habitat factors that covary with fire-history variables to explain reptile responses. We hypothesise that more complex habitats should support richer reptile communities, and that species-specific relative abundance should be related to particular habitat features. From spring 2012–2014, twenty-five transects were surveyed in the Albera Region (north-east Iberia). The vegetation structure was measured and the extent of habitat types in a 1000-m buffer around each transect calculated. Reptile-community metrics (species richness and reptile abundance) were related to fire history, vegetation structure, and habitat types, using generalized additive models. These metrics correlated with habitat-structure variables but not with fire history. The number of species increased with more complex habitats but decreased with pine-plantation abundance in the 1000-m buffer. We

found contrasting responses among reptiles in terms of time since fire and those responses differed according to vegetation variables and habitat types. An unplanned fire in August 2012 provided the opportunity to compare reptile abundance values between pre-fire and the short term (1–2 years) after the fire. Most species exhibited a negative short-term response to the 2012 fire except *Tarentola mauritanica*, a gecko that inhabits large rocks, as opposed to other ground-dwelling species. In the reptiles studied, contrasting responses to time since fire are consistent with the habitat–accommodation model of succession. These differences are linked to specific microhabitat preferences and suggest that functional traits can be used to predict species-specific responses to fire.

**Keywords** Disturbance · Repeated-fire regime · Reptiles · Habitat–accommodation model · Microhabitat preferences

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## Introduction

Fire is a common form of disturbance in many regions of the world (Moritz et al. 2012) and a key driver of ecosystem function (Bond et al. 2005). In fire-prone ecosystems, the response of animal communities to fire is driven primarily by habitat characteristics, i.e. vegetation structure and composition (Briani et al. 2004; Madden et al. 1999; Valentine and Schwarzkopf 2008; Nimmo et al. 2014). Consequently pre- and post-fire habitats support different animal communities across a wide range of taxa [e.g. snails (Santos et al. 2009), bees (Moretti et al. 2009), ants (Arnan et al. 2013), reptiles (Driscoll and Henderson 2008), and birds (Brotons et al. 2008)]. Habitat transformation through the post-fire succession may alter the composition of animal communities over time. This ‘habitat–accommodation model’ of

succession (Fox 1982) proposes that species colonize an area when their preferred habitat type has developed and their numbers then decline as plant succession proceeds beyond their optimal habitat conditions.

In reptiles, a number of studies have failed to find 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). For example, empirical studies by Lindenmayer et al. (2008) conjectured that the lack of support for the habitat-accommodation model may be due to the fast recovery of key vegetation components in certain ecosystems. However, most field-based studies report that the relative abundance of many species varies according to time since fire (Nimmo et al. 2012; Smith et al. 2013), implying that some species tend to prefer early or late-successional habitats (Letnic et al. 2004; Santos and Poquet 2010; Valentine et al. 2012). A recent study by Nimmo et al. (2014) proposed that regional variation in fauna–fire relationships signifies that the habitat–accommodation model may be conceptually accurate but predictively weak at large spatial scales. Smith et al. (2012) suggested that detailed measures of habitat structure and use may improve our understanding of how reptile communities respond to fire.

In addition, life history traits of species (e.g. dietary habits, reproduction, longevity, habitat selection, and dispersal patterns) can also help to elucidate reptile responses to fire (Smith et al. 2012, 2013). This functional approach has been developed in other taxa (Moretti et al. 2006, 2009; Arnan et al. 2013; Santos et al. 2014). In reptiles, Santos and Cheylan (2013) detected a functional response to fire, habitat preference being one of the traits involved. Due to their thermal constraints and specialization (Huey 1982), some reptile species may be adapted to more simplified habitats than the types found in early post-fire succession. When their micro-habitats are not directly destroyed by fire (e.g. cliff-dwelling species) these species may show a short-term response. Thus, microhabitat preference may be a relevant factor to understand the response of reptiles to fire (Smith et al. 2013).

Our study examines the response of reptiles to fire history (time since fire and number of fires) and to habitat covariates such as vegetation structure and habitat types. Considering that this group consists of ectotherm organisms, we seek to identify reptile responses to fire history (time since fire and number of fires) and also to changes in canopy, habitat heterogeneity, and ultimately thermal quality related to solar radiation. Fires reduce vegetation, leading to more habitat complexity with time since fire; accordingly, more complex habitats are hypothesised to support richer reptile communities. Likewise, the relative abundance of some species should vary in relation to particular habitat features.

We have examined these issues in a protected Mediterranean area in the north-eastern Iberian Peninsula that has been affected by multiple fire events in the last 30 years. During the fieldwork, an unplanned fire burned part of the study area in August 2012, providing an opportunity to examine short-term responses to fire by comparing the pre-fire and immediate post-fire (1 and 2 years after the fire) relative abundance of reptiles [see a similar case in Lindenmayer et al. (2014) for birds].

The main objective of our study was to explore the habitat and fire-history factors which drive reptile responses at the community (species richness and total abundance) and species (relative abundance of species) levels. Specifically, we addressed the following questions:

1. Are species richness and abundance related to time since fire and number of fires?
2. Are species richness and abundance related to particular factors of the vegetation structure and habitat types?
3. Within the reptile community, are there inter-specific differences in their response to fire history and habitat features?
4. Are these inter-specific differences related to particular life history traits of species such as habitat preference?

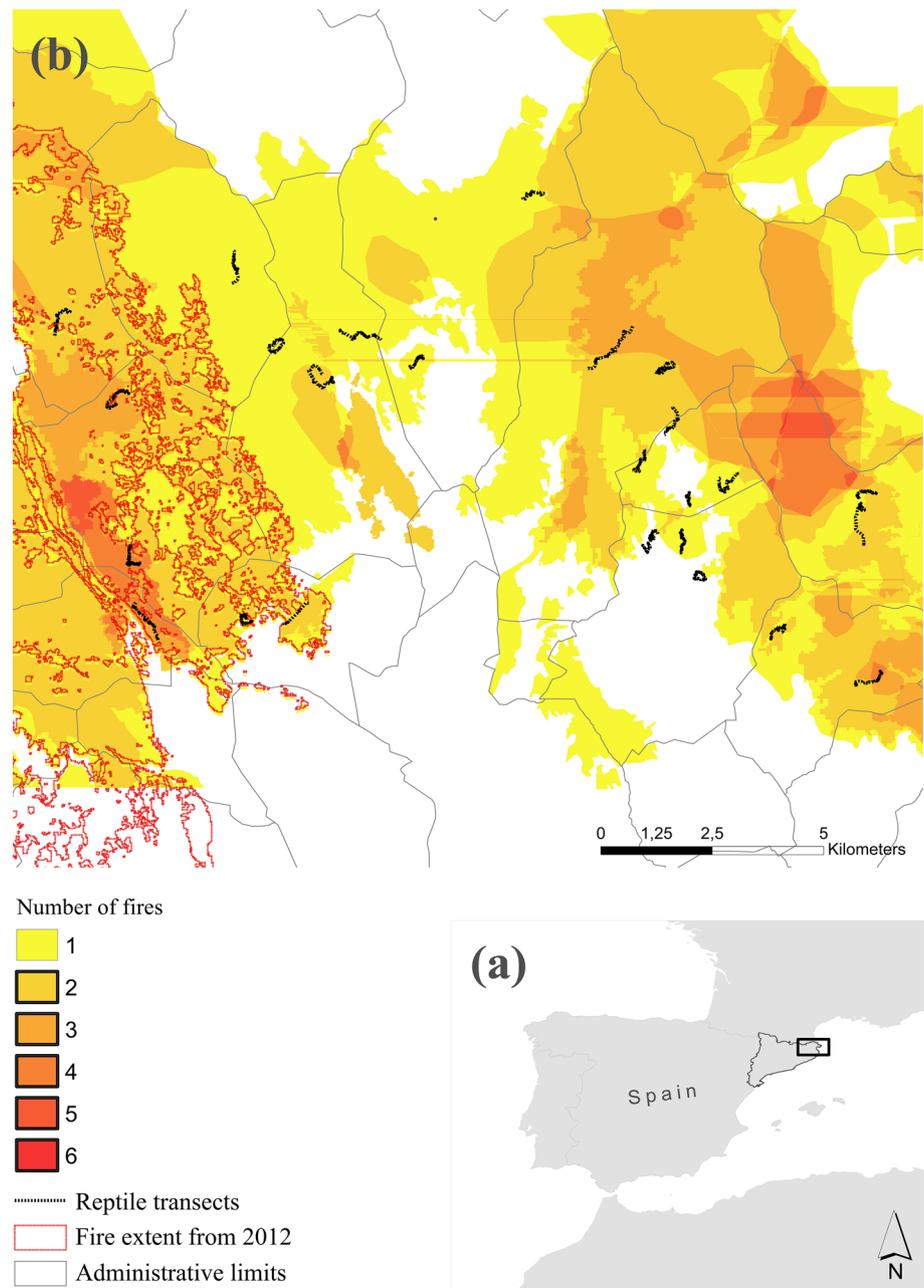
## Materials and methods

### Study area

The study was conducted in the lowlands of the Albera Massif in the north-eastern Iberian Peninsula (Fig. 1a). Located along the foothills of the eastern Pyrenees, this region is characterized by a typical Mediterranean climate and vegetation. Rainfall averages between 500 and 600 mm and this area is heavily influenced by the Tramontane, a dry wind from the north. In the lowlands, the main vegetation type is a mixture of open scrubland and evergreen oak forests dominated by the cork oak *Quercus suber*. However, the landscape reflects a long history of human presence in the region. During the early twentieth century, the study area was covered mainly by vineyards. After the phylloxera plague in the mid-twentieth century, new cork oak plantations partially recovered a natural landscape (J. Budó, personal communication). Currently, the landscape is a mixture of natural vegetation interspersed with agricultural land, mainly cereals and vineyards, and pine plantations. Part of the study area is protected by the Paratge Natural d'Interes Nacional de la Albera and Natura Web 2000 since 1986 and 2006, respectively.

The Albera Massif has a long fire history. Due to the Mediterranean climate, the Albera lowlands are affected by a crown fire regime. Fire occurrence peaks in summer due

**Fig. 1** Location of the study area in the Iberian Peninsula (a), and distribution of the 25 transects sampled (black lines) in relation to the number of fires (b). **b** The area covered by the August 2012 fire is approximately 10,000 ha



to drought conditions. In the past 60 years large-scale fires were recorded in 1978, 1986, 2000, and 2012. The area is a patchy mosaic of sites characterized by different habitat types varying in time since the last fire.

### Sampling design

Reptiles were sampled in a series of natural experimental transects by time-constrained 1-h trails at 25 sites (Fig. 1b). Transect length averaged  $1252 \pm 64$  m, and the minimum polygon including all transects covered a 100-km<sup>2</sup> area of the Albera Massif. Transects were established in lowlands

(mean altitude 199 m, and range 83–388), rather than in mountains, where vegetation and reptile assemblages are different due to the combined effects of altitude and climate (Llorente et al. 1995). Selectively located in large patches of natural vegetation, mainly *Q. suber* forest, the transects were usually surrounded by other habitat types. Also, the transects were situated on south-facing slopes to avoid biases in reptile composition due to sun exposure.

Transects were placed on trails where reptile detectability was easier. Each transect was first tracked with a global positioning system device in order to follow the same path during the subsequent visits. Each transect was surveyed

from five to eight times in order to increase the likelihood of including reptile species of low detectability. Each survey was carried out by one researcher during spring 2012 (April–June), 2013 (April–May), and 2014 (April) when reptile activity was high. During surveys, the researcher visually searched for reptiles, turning over rocks and investigating other potential refuges. This method has been shown to be adequate for assessments of relative abundance and presence of the commonest Mediterranean reptile species (Santos and Cheylan 2013). All individuals sighted were identified to the species level and georeferenced. We used the updated reptile nomenclature accepted by the Spanish Herpetological Society ([www.herpetologica.es](http://www.herpetologica.es)).

### Ecogeographical variables

For each transect, we collected information on fire history, vegetation structure, and habitat types [Electronic supplementary material (ESM), Table A1]. Within these categories, we measured a set of ecogeographical variables (EGV) that are potential predictors of presence/absence and abundance of reptile species:

1. Fire history. The number of fires and time since last fire (LASTFIRE) at each transect (ESM, Table A2) were extracted from the Prevention Plan for the Fire Forest in the Albera Massif provided by the Agriculture Department (government of Catalonia). Fire events are here summarized from 1950 until the present time. The first fire registered for our study area occurred in 1973 (ESM, Table A2).
2. Vegetation structure. Plant composition and habitat structure of transects were characterized by recording the abundance of plant types (i.e. grass, shrubs, and trees) and vegetation height along a 100-m transect within the reptile transect. Plant types were recorded at points 1-m apart along the 100-m transect. From these 100 points, we calculated the relative abundance of grass, shrubs, and trees. At each 1-m point, vegetation height was also measured with a tape measure, and the mean vegetation height for the 100-m transect calculated. Finally, we constructed a matrix of grass, shrub, and tree relative abundance as well as a matrix of relative-abundance values for the 1-m height classes. From these two matrices, we calculated Pielou's evenness (plant-type abundance evenness, and height class evenness). These indexes quantify the degree of numerical equality in each transect; therefore, higher evenness scores indicate more complex (heterogeneous) transects in terms of plant composition and habitat height.
3. Habitat types. Spatial information was gathered from two different sources: (a) a map from agricultural zones in 1956 drawn from the aerial photographs taken in the

same year, and (b) land-use maps between the years of 1979/1980 with a 1:50,000 resolution. At the sites, we checked the degree to which the current land uses were accurately reflected by these maps. According to the natural/artificial origin and vegetation type, five main habitat classes were established: *Q. suber* forest, *Pinus* sp. forest, scrubland, grassland, and non-natural habitats, the latter including vineyards, crops, and urbanized lands. We calculated the extent of each habitat class in a 1000-m buffer around each transect. From the matrix of relative-abundance values of habitats at 1000-m buffers, we calculated Pielou's evenness of each transect to measure the level of habitat heterogeneity around the transects.

All spatial analyses were performed with ArcGIS 10.x (ESRI 2011) and Quantum GIS Desktop 1.8.0 (Quantum GIS Development Team 2011).

### Short-term responses to fire

In August 2012, an unplanned fire burned part of the study area and affected six out of the 25 transects previously sampled in spring 2012 (Fig. 1b), enabling us to compare the reptile composition and abundance before and after the August 2012 fire. The six burned transects were grouped into two categories according to their previous fire history: three of them had previously burnt two or three times, the other three only once. Six unburnt transects in 2012 were selected as control sites. All these transects were sampled in spring 2013 and 2014, i.e. 1 and 2 years after the 2012 fire. The short-term response of reptiles to fire was examined by comparing changes in species richness and abundance before and after the 2012 fire.

### Data analysis

Three community metrics were used to assess the response of the reptile community to fire: species richness, reptile abundance, and Pielou's evenness. As the sampling effort between transects (number of visits) was not the same, species richness and reptile abundance were calculated as the average number of species and reptiles recorded per visit within each transect. At the species level, we examined the response of each reptile species to fire by calculating the average number of individuals recorded per visit within each transect.

We calculated the pair-wise correlation of fire-history with vegetation and habitat variables. This preliminary analysis determined whether fire drives habitat changes, and therefore the potential effect of both types of variables can represent the same phenomenon. Pair-wise correlations were calculated with a non-parametric *R* Spearman test due to the non-normal distribution of the LASTFIRE variable.

The relative importance of fire-history, vegetation-structure, and habitat-type variables for predicting reptile responses (reptile abundance, species richness, reptile evenness, and the abundance of four reptile species) was explored using general additive models (GAMs). We used GAMs rather than assuming linear fits. This approach is considered a more flexible framework as the relationship between environmental and fire variables against reptile metrics and species abundance can be fitted as either non-linear or linear terms (Valentine et al. 2012; Hu et al. 2013; Nimmo et al. 2014).

Due to the low number of sampled transects ( $n = 25$ ), we generated GAMs for each group of predictors separately (fire history, vegetation structure, and habitat types), with no interactions between variables. We produced 21 models (3 groups of EGV predictors  $\times$  7 dependent reptile variables) and within each model we examined which EGVs significantly correlated to the dependent variables. GAM procedures use smoothing splines, and parameter estimates could not be modelled in a way equivalent to that used for generalized linear models (GLMs). We used the deviance explained by each model as the measure of model fit. Smoothed terms of each predictor variable were considered significant when  $P < 0.05$ . Prior to the model analysis, data were tested for normality and variability (outliers) (Zuur et al. 2010). Given the non-normal distribution and high variability in scores of the dependent variables (reptile abundance, species richness, reptile evenness, and the abundance of each reptile species), a Poisson distribution with overdispersion correction (quasi Poisson family) was used to fit models. GAM analyses were performed using packages ggplot2 (Wickham 2009), MASS (Venables and Ripley 2002), mvoutlier (Filzmoser et al. 2005), mgcv (Wood 2013), and nlme (Pinheiro and Bates 2000) from the statistical programming software R (R Core Team 2014).

Short-term responses of species richness and reptile abundance per transect, and the relative abundance of *Tarentola mauritanica* and *Psammodromus algirus* lizards (the commonest species in the study area) were examined with GLMs; year (2012, 2013 and 2014) and the 2012-fire condition (burnt and unburnt) were used as grouping variables. We also examined the interaction between the two factors. For each of the four dependent variables, the Wald  $\chi^2$  statistic was computed to check the average variation among groups, the parameter estimates, and the statistical significance of the variation.

## Results

### Survey results

In total, we observed 856 reptiles from nine species including two tortoises, five lizards, and two snakes. Combining relative-abundance values of species and the percentage

**Table 1** Number of individuals ( $n_1$ ) and number ( $n_2$ ) and percentage of transects where each reptile species was detected

Family	Species	Abbreviation	$n_1$	$n_2$	%
Testudinidae	<i>Testudo hermanni</i>	THE	52	12	48
Bataguridae	<i>Mauremys leprosa</i>	ML	2	1	4
Geckonidae	<i>Tarentola mauritanica</i>	TAM	155	23	92
Lacertidae	<i>Psammodromus algirus</i>	PSA	560	25	100
	<i>Timon lepidus</i>	TL	45	18	72
	<i>Podarcis liolepis</i>	PL	10	3	12
Scincidae	<i>Chalcides striatus</i>	CS	18	11	44
Colubridae	<i>Malpolon monspessulanus</i>	MM	15	13	52
	<i>Rhinechis scalaris</i>	RS	1	1	4

of transects with occurrence, four out of nine species can be considered common in the study area (Table 1). The commonest species was the psammodrome lizard *P. algirus*. According to Sillero et al. (2009) this reptile community in the Albera lowlands is typically Mediterranean as all species have almost their entire distribution within the Mediterranean ecoregion. During transect observations, we detected 75 % of species previously described for the study area (Llorente et al. 1995; J. Budó, unpublished data). Only three snakes were not found in the transects, two of them being water snakes of the genus *Natrix*.

### Pair-wise correlations between EGVs

Pair-wise correlations of fire-history variables with vegetation and habitat variables showed some relationships (Table 2). Transects with high values for time since fire had more tree abundance and low shrub abundance. Moreover, these transects had greater canopy height and constituted more complex habitats, i.e. higher evenness values (Table 2). The number of fires per transect also evidenced some correlation with greater shrub abundance.

### GAM results for reptile metrics

None of the metrics examined for the reptile community (species richness, species evenness, and reptile abundance) correlated to fire-history factors. We found a pattern of increased species richness with time since fire (ESM, Fig. A1), although the correlation was not significant ( $p = 0.09$ ), perhaps due to the few number of transects examined. By contrast, strong correlations with several vegetation-structure variables were observed with reptile-community metrics (Table 3) with explained deviance values ranging from 64.9 to 92.9 % (ESM, Table A3). For example, species richness and evenness increased in habitats with the highest (i.e. forests) and the lowest (i.e.

**Table 2** Pair-wise Spearman correlation tests ( $R$ -values) of the fire-history variables [number of fires ( $N\_FIRES$ ) and time-since-fire ( $LASTFIRE$ )] with vegetation and habitat variables

Vegetation and habitat variables		$N\_FIRES$	$LASTFIRE$
Code	Description		
AB_GRASS	Relative abundance of grass	-0.100	0.056
AB_SHRUB	Relative abundance of shrub	0.443*	-0.525**
AB_TREES	Relative abundance of trees	-0.332	0.543**
HE_VEGET	Mean vegetation height	-0.316	0.589**
AB_EVEN	Plant-type abundance evenness	0.195	-0.252
HE_EVEN	Plant height-class evenness	-0.248	0.501*
H_QUERC	<i>Quercus suber</i> forest	-0.272	0.194
H_PINE	<i>Pinus</i> sp. forest	0.283	-0.269
H_NONNAT	Non-natural habitat	-0.178	0.055
H_SHRUB	Scrubland	0.414*	-0.279
H_GRASS	Grassland	-0.333	0.393
H_EVEN	Habitat-type Pielou's evenness	-0.431*	0.297

\*  $p < 0.01-0.05$ , \*\*  $p < 0.001-0.01$ , \*\*\*  $p < 0.001$

grasslands) vegetation heights (Table 3, Fig. 2a, b, respectively). Reptile evenness also correlated with height-class evenness, as the complexity of reptile communities

increased in more complex habitats (Fig. 2c). Species richness diminished with pine abundance in the 1000-m buffer surrounding transects (Table 3; Fig. 2d). Finally, reptile abundance increased when the area covered by *Q. suber*, scrubland and non-natural habitat types increased (Figs. 2f, g, and 3, respectively).

### GAM results for species abundance

The relative-abundance values of several species were found to be correlated to time since fire (Table 3), with explained deviance values ranging from 31.8 to 94.2 % (ESM, Table A3). However, responses were opposite: *Testudo hermanni* and *Timon lepidus* abundance increased whereas that of *Tarentola mauritanica* declined with time since fire (Fig. 3a–c, respectively). *T. lepidus* abundance also increased with the number of fires (Table 3; Fig. 3d). Hermann's tortoise *T. hermanni* responded positively to higher habitat complexity [plant height-class evenness (HE\_EVEN), Fig. 4a] but negatively to non-natural habitats in 1000-m buffers surrounding transects (Table 3; Fig. 4b). The relative-abundance values of the three lizard species *P. algirus*, *T. mauritanica*, and *T. lepidus* positively correlated to the increase in *Q. suber* forest area in the 1000-m buffer (Table 3, Fig. 4c–e, respectively).

**Table 3** Summary of the predictive variables that correlated with reptile community metrics and species relative abundance after running general additive model analyses

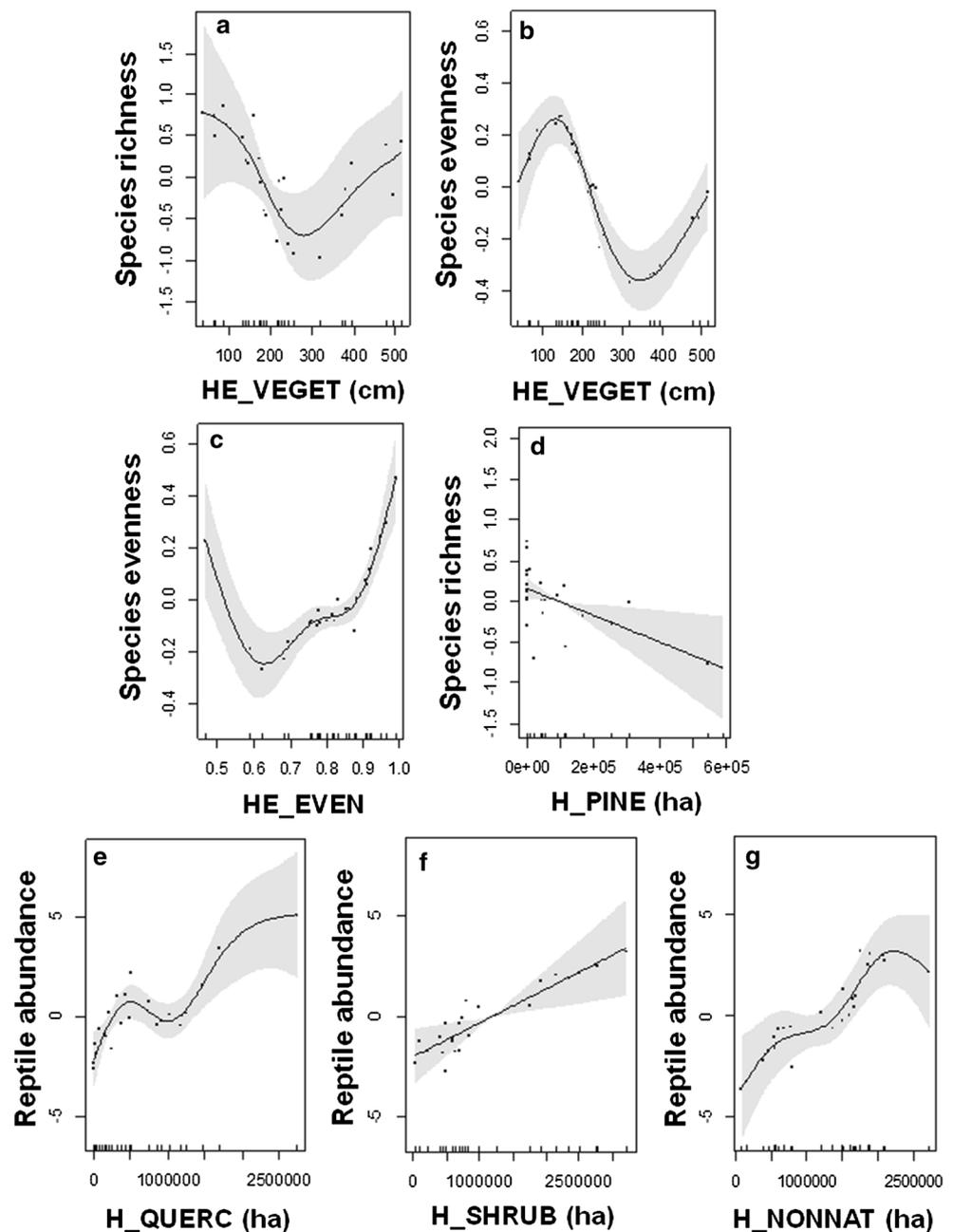
	Fire history				Vegetation structure				Habitat uses			
	Factor	Edf	F	p	Factor	Edf	F	p	Factor	Edf	F	p
Reptile abundance									H_QUERC	3.83	4.27	*
									H_SHRUB	1.00	8.17	*
									H_NONNAT	3.71	4.77	*
Species richness					HE_VEGET	3.46	3.25	*	H_PINE	1.00	6.529	*
Species evenness					AB_GRASS	1.00	16.79	**				
					AB_SCRUB	1.00	12.30	**				
					HE_EVEN	4.00	13.13	***				
					HE_VEGET	3.91	10.41	***				
<i>T. hermanni</i> abundance	LASTFIRE	1.09	9.75	**	AB_SCRUB	1.00	12.90	**	H_NONNAT	3.95	3.93	*
					HE_EVEN	3.89	7.71	**				
					HE_VEGET	3.94	8.67	**				
<i>P. algirus</i> abundance									H_QUERC	1.00	5.23	*
<i>T. mauritanica</i> abundance	LASTFIRE	1.00	9.99	**					H_QUERC	1.00	5.98	*
									H_SHRUB	3.93	6.86	**
									H_NONNAT	1.00	6.07	*
<i>T. lepidus</i> abundance	$N\_FIRES$	1.00	9.54	**					H_QUERC	1.00	7.52	*
	LASTFIRE	1.00	13.29	**								

Only significant correlations are shown

Edf Effective df; for other abbreviations, see Table 2

\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$

**Fig. 2** Response curves from significant general additive model (GAM) relationships of reptile community metrics and the environmental variables analysed. *Shaded area* represents  $\pm 95\%$  confidence intervals. *HE\_VEGET* Mean vegetation height, *HE\_EVEN* plant height-class evenness, *H\_QUERC* *Quercus suber* forest, *H\_PINE* *Pinus* sp. forest, *H\_SHRUB* scrubland, *H\_NONNAT* non-natural habitats



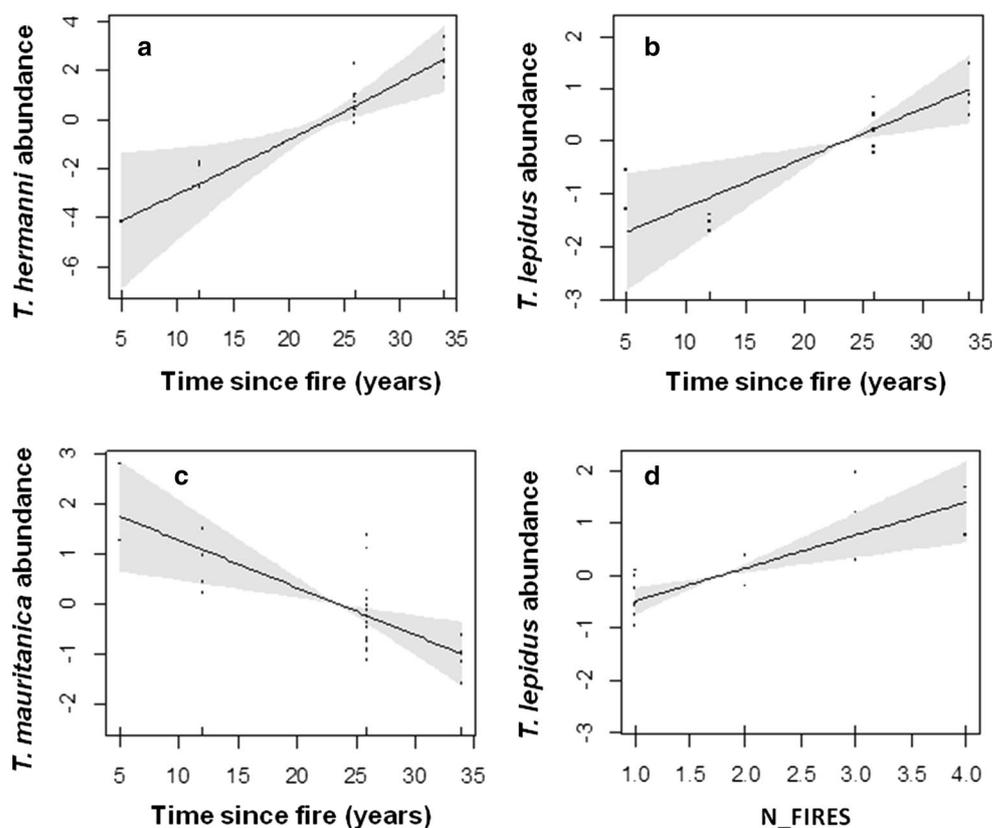
### Short-term response of reptiles to fire

GLM analyses demonstrated that species richness, reptile abundance, as well as relative abundance of *T. mauritanica* and *P. algirus* lizards did not vary between years (Table 4). Species richness was higher in transects that did not burn in August 2012 (Table 4). When we examined the interaction between the factors year and burnt in August 2012, we found significant differences (Table 4): the transects affected by a recent fire in August 2012 showed a reduction in species richness and reptile abundance from spring 2012 to spring 2013 (Fig. 5a, b, respectively). In contrast, we

did not detect this trend in the control transects not burnt in 2012. In 2014, however, reptile abundance increased in some transects that had burned in 2012 (Fig. 5b), suggesting a fast recovery 2 years after the fire.

According to the GLM, the interaction between the factors year and burnt in August 2012 also showed differences for the ground-dwelling lizard *P. algirus* (Table 4). There was a reduction in lizard abundance from 2012 to 2013 in transects affected by the August-2012 fire, but values recovered in 2014. We found no variation from 2012 to 2014 in unaffected transects (Fig. 5c). On the contrary, the gecko *T. mauritanica*, a species inhabiting cliffs, large

**Fig. 3** Response curves from significant GAM relationships of species-abundance and fire-history variables analysed. Shaded area represents  $\pm 95\%$  of confidence intervals. *N\_FIRES* Number of fires



rocks, and buildings, displayed no difference in abundance over the sampling period (Table 4; Fig. 5d).

## Discussion

### Responses at the reptile-community level

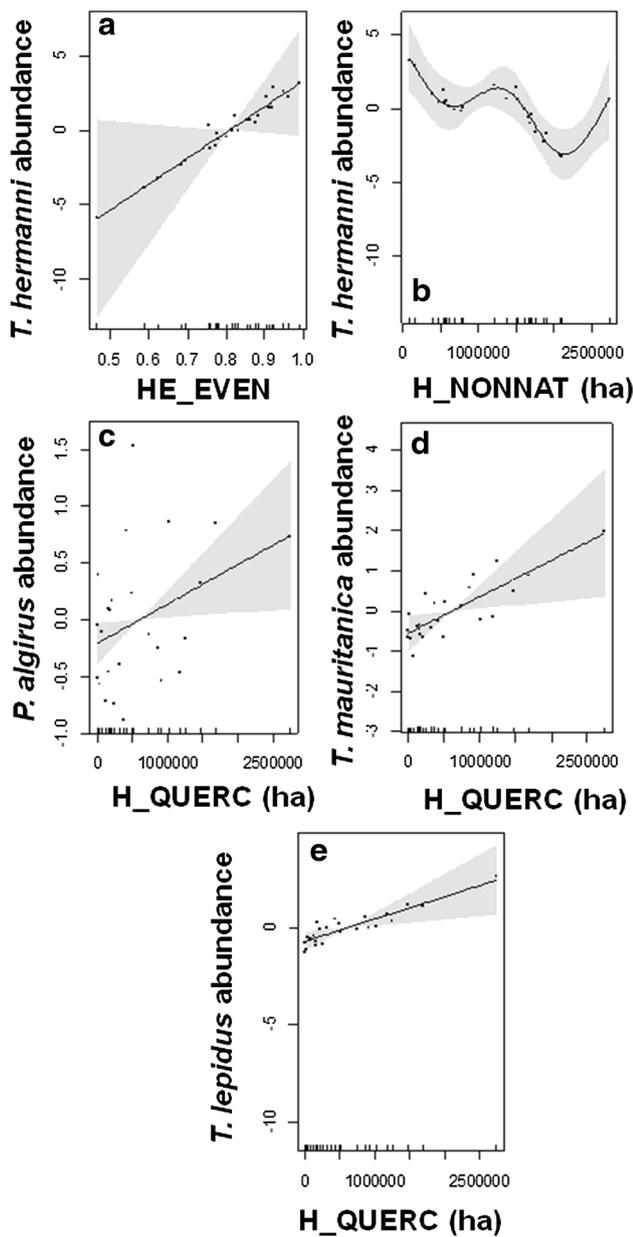
At the community level, no fire-history or vegetation-structure variables correlated with species richness and reptile abundance. Rather, these community metrics decreased with the surface area of pine woodlands in 1000-m buffers around the transects. *Pinus* sp. is the most extensive tree genus used in reforestation throughout the Mediterranean basin (Blondel et al. 2010). Our results indicate that it is a low-quality habitat for reptiles (Azor et al. 2015), as detected in a higher geographic range (Ribeiro et al. 2009) as for other taxa (Mateos et al. 2011; Torre et al. 2014).

Our study failed to find a clear relationship between fire history and reptile species richness. Several studies have highlighted the impact of fire on the reptile community, either in the Mediterranean basin (Santos and Cheylan 2013) or in other fire-prone regions such as temperate, semi-arid, and arid Australian regions (Letnic et al. 2004; Lindenmayer et al. 2008; Valentine and Schwarzkopf 2008; Nimmo et al. 2012, 2013; Pianka and Goodyear 2012;

Valentine et al. 2012). We found no evidence of a time-since-fire effect on the overall reptile assemblage in the Albera region. We could argue that species richness did not vary with time since fire due to a species replacement from early to late post-fire colonizers. Large-scale fires that burned a significant part of the Albera range occurred at rather regular time intervals (in 1978, 1986, 2000 and 2012). In this scenario, some areas remained unburnt for more than 30 years (ESM, Table A2), and these held the richest reptile communities (ESM, Fig. A1). Although we found a pattern for increasing species richness with time since fire (these results are consistent with the decline in species richness immediately after the 2012 fire), GAM results found weak support for this correlation perhaps due to the low number of transects sampled. The complexity of environmental processes that operate simultaneously to drive reptile responses to fire (Pastro et al. 2013) also could obscure a clearer relationship between community metrics and fire history.

### Responses at the species level

Our study detected a response to time since fire for some species-specific abundance values. Notably, these responses differed among species, with an increase for *T. hermanni* and *T. lepidus* and a decrease for *T. mauritanica*.



**Fig. 4** Response curves from significant GAM relationships of species abundance, vegetation structure, and habitat classes analysed. Shaded area represents  $\pm 95\%$  confidence intervals. For abbreviations, see Fig. 2

**Table 4** Generalized linear model results of differences in species richness (# SP), reptile abundance (# Reptiles), and relative abundance of PSA and TAM for the 3 years sampled (2012–2014), and the burnt condition after the 2012 fire, and their interaction

	# SP		# Reptiles		PSA		TAM	
	Wald stat.	<i>p</i>						
Year	2.57	NS	3.24	NS	3.10	NS	3.60	NS
2012-fire	15.84	<0.0001	0.08	NS	0.45	NS	1.19	NS
Year $\times$ 2012-fire	8.81	0.01	5.69	0.06	6.47	0.04	0.07	NS

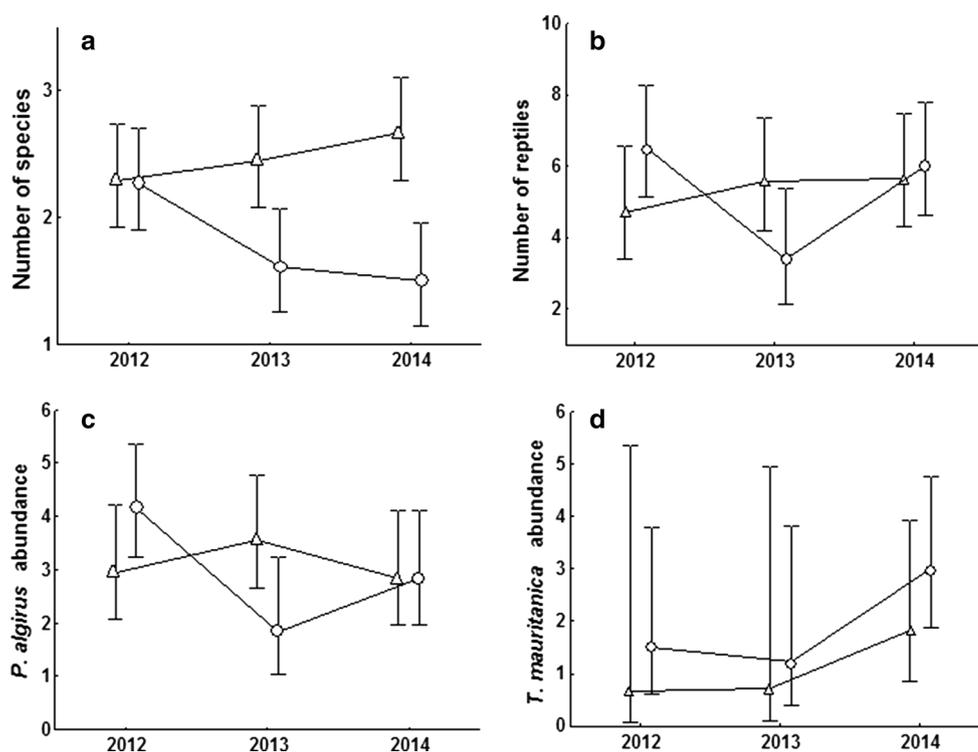
For each dependent variable, the Wald  $\chi^2$  statistic (*stat.*) and *p*-value are shown. For other abbreviations, see Table 1

The impact of fire on the Hermann’s tortoise *T. hermanni* has previously been reported on a larger geographic scale (Couturier et al. 2014) and is clearly related to the high mortality inflicted by fire (Fèlix et al. 1989; Hailey 2000), as well as to particular life history attributes that make this tortoise vulnerable to repeated fire regimes (Couturier et al. 2011; Santos and Cheylan 2013). GAM results for *T. hermanni* also indicated that its abundance increased with more complex (higher plant height-class evenness) and mature (higher mean vegetation height) habitats. Thus, *T. hermanni* can be classified as a late post-fire successional species. In a scenario of increased fire frequency (McKenzie et al. 2004), late successional habitats may be dramatically reduced, causing local extinction of late colonizers (Valentine et al. 2012). This may be the case of *T. hermanni* in the Albera region, where large fires tend to occur every 10 years.

The negative correlation observed for *T. mauritanica* abundance and time since fire matches its short-term responses observed after the August 2012 fire. The field-work conducted in 2013 demonstrated that all reptile species except *T. mauritanica* had a negative short-term response to fire. This gecko is the only species that occupies large rocks, cliffs, and buildings in the Albera range. We argue that its microhabitat specialization might account for its short-term response. Contrarily, the understory specialist lizard *P. algirus* drastically declined over the short-term as it was potentially more affected by severe vegetation shifts after fire. In Australia, Smith et al. (2012) observed that burrowing species have lower mortality than non-burrowers during wildfires. Microhabitat preference seems hence a valuable species trait in predicting the short-term response of reptiles to fire (Santos and Cheylan 2013).

At the species level, GAM results also indicated a positive correlation of relative abundance of some reptiles with particular habitat classes in the 1000-m buffer surrounding transects. Notably, several species increased with the surface area of cork oak *Q. suber*. These trees represent the most extensive natural woodland in the study area, and a traditional economic source for cork manufacture (Alvarado 2002). The protection of this woodland seems important for the maintenance of the high relative abundance of certain reptile species. Notably, the extent of non-natural

**Fig. 5** Yearly variation in the predicted species richness (a), reptile abundance (b), relative abundance of *Psammodromus algirus* (c) and *Tarentola mauritanica* (d) according to the generalized linear model results. Symbols represent the predicted mean interaction of year and burnt condition in August 2012, and whiskers 95 % confidence intervals. Triangles Transects not burnt in 2012, circles transects burnt in 2012



habitats was positively correlated to *T. mauritanica* and negatively to *T. hermanni*. These divergent responses indicate that heterogeneous landscapes with open areas and woodlands might maximize  $\beta$ -diversity of the reptile community. Similarly, patchy habitats from a range of fires (Valentine et al. 2012) or the extent of long-unburnt areas (Farnsworth et al. 2014) have been identified to increase  $\beta$ -diversity of other reptile communities.

#### Fire and habitat correlations and the habitat–accommodation model of succession

Significant correlations of fire history with vegetation and habitat variables demonstrated that, in the Albera Range, fire models the habitat structure and plant composition. In turn, these effects on the habitat prompt reptile responses, as evidenced by GAM results. Thus, the relationship between reptiles and vegetation is also related to fire effects. At the community level, we found weak evidence for the correlation between species richness and fire history, vegetation structure, and habitat uses [except the negative response to the surface area of pine recently demonstrated by Azor et al. (2015) in the Mediterranean basin]. At the species level, however, we detected divergent results in the short-term response to fire and time since fire. These distinctive responses suggest that these species peak at different post-fire successional stages, as reported in other reptile communities (Pianka and Goodyear 2012; Smith et al. 2013; Nimmo et al. 2013). This result supports the

habitat–accommodation model of succession for the reptile community in the Albera Range.

Moreover, we found that the response to fire was related to particular habitat preferences of species. Nimmo et al. (2014) stated that the habitat–accommodation model of succession, although conceptually accurate, was predictively weak. Incorporating functional traits could make it possible to refine this model as a predictive tool to be applied in fire-prone regions worldwide. Unfortunately, attempts to build a comprehensive trait-based model of succession found only limited support (Smith et al. 2013). This weak support may be motivated by the multidimensionality of the ecological niche. In this sense, ecological (biotic) interactions need to be explored in the future to improve knowledge on the mechanisms involved in functional responses of organisms to fire (Letnic et al. 2004).

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