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Taxonomic and functional response of a Mediterranean reptile assemblage to a repeated fire regime

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ABSTRACT

Wildfires are common disturbances that have a major impact on ecosystems. Recent decades have seen an increase in fire frequency and extension due to the combined effects of climate change and land-use history. We studied the taxonomic and functional response of a reptile assemblage to repeated fires in southern France to understand shifts in dominant species and diversity, as well as the mechanisms that underlie responses according to functional traits of species. In the spring of 2010, we sampled reptiles in areas with three types of fire regime: unburned, burned once (2003) and burned 4–5 times (last fire in 2003) along a fire history of 51-years period. With this field sampling design, we examined the intermediate disturbance hypothesis and the habitat accommodation model of succession as methods to predict reptile responses to natural fire regimes. We also compared habitat structure at the study area between 1944 and 2006 to certify that repeated-fire regimes have modified the habitat for reptiles. The comparison of the habitat structure between both periods demonstrated that repeated-fire regimes modified the landscape from a homogeneous sparse forest to a contrasted heterogeneous mixture of scrubland and dense forest. We found a loss of reptile diversity after one and multiple fires, a result that contradicts the intermediate disturbance hypothesis. Reptile composition differed among the three fire regimes: there was a shift in dominant species and a reduction of beta diversity related to an increase in the number of fires. We also observed a functional response to repeated fires, with an increased frequency of insectivorous reptiles, which live in open areas, are specialists in their ecological niche, and have a short lifespan. These results suggest that reptile replacement according to fire regime accounts for a habitat accommodation model following particular traits of species. Our study indicated that areas subjected to repeated fires have a more strictly Mediterranean reptile assemblage than unburned areas, due to the ability of Mediterranean species to survive thermal environments in open (burned) areas. At a regional scale, changes in dominant species between unburned and repeatedly burned areas might be an argument for maintaining a patchwork of areas burned at variable intervals. However, the increase in fire frequency and extension suggests a future scenario of extinction for species negatively impacted by fire, such as the endangered Hermann's tortoise *Testudo hermanni*, for which the study area is home to one of the last native populations in the western Mediterranean.

1. Introduction

Understanding the response of species to environmental change is a major goal in predicting its effects on biodiversity (Hooper et al., 2005). Wildfires are considered among the disturbances that have a major impact on ecosystem functioning and composition in many areas of the world (Bond et al., 2005). Fire act as an environmental filter selecting these species better adapted to the narrow post-fire environmental conditions (Pausas and Verdú, 2008), and consistently, species may be adapted to this natural disturbance in prone-fire regions. Thus, it is possible to build a model to predict animal responses to fire as a function of particular habitat requirements (Nimmo et al., 2012). Empirical studies show that the response of organisms to fire is complex, often resulting in species-specific responses within a single taxonomic group [e.g. ants (Rodrigo and Retana, 2006), amphibians (Pilliod et al., 2003), reptiles (Driscoll and Henderson, 2008; Lindenmayer et al., 2008; Santos and Poquet, 2010), and arthropods (Moretti et al., 2004, Moretti et al., 2006)]. These inconsistent results suggest that response to fire can vary greatly according to intrinsic factors of

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organisms (e.g. functional traits, Moretti et al., 2009), as well as extrinsic factors such as fire regime (Moreira and Russo, 2007) and severity (Pausas et al., 2002), environmental gradients (Arnan et al., 2006), climatic region (Moretti et al., 2009), pre-fire habitat type (Rodrigo et al., 2004, 2008), and post-fire management (Castro et al., 2010).

The intermediate disturbance hypothesis and the habitat accommodation model of succession have been examined as methods to predict biotic responses to natural fire regimes (Driscoll and Henderson, 2008; Lindenmayer et al., 2008). The first states that biodiversity increases at localities subjected to intermediate rates of disturbance (Connell, 1978), and the second suggests that communities recover following disturbance linked to the recovery of habitat structure (Fox, 1982). In fire-adapted regions such as the Mediterranean, biota and ecosystems are highly dynamic and resilient (Blondel et al., 2010), then expecting empirical support of biotic responses to the intermediate disturbance hypothesis and the habitat accommodation model of succession. However, resilience varies according to the nature and the complexity of the habitat (Westman and O'Leary, 1986; Jacquet, 2006), and an increase in fire frequency prevents mature ecosystems from returning to their pre-fire state, maintaining it in earlier successional stages (Mouillot et al., 2003). Thus, the interval between consecutive fires plays a major role in the Mediterranean community's resilience capacity (Keeley, 1986; Eugenio et al., 2006). In the region's plant communities, several authors have reported resprouting difficulties (Eugenio and Lloret, 2004) and decreasing resilience patterns (Díaz-Delgado et al., 2002; Vilà-Cabrera et al., 2008) following recurrent wildfires. As wildfires promote scrubland and herbaceous expansion to the detriment of forests (Pausas and Vallejo, 1999; Vilà-Cabrera et al., 2008), this may result in a parallel shift in animal groups, a pattern that could be more intense after repeated fires. Given the strong association between plant and animal responses in fire-disturbed areas (Moretti and Legg, 2009), we would expect repeated fires to generate profound shifts in species composition in parallel with changes in vegetation structure.

We examined the response of a reptile assemblage of a locality with a repeated fire regime in southern France assessing reptile abundances in unburnt, once burnt and repeated burnt transects. Fire usually improves the habitat for reptiles (Bury, 2004); as a consequence, several species take advantage of post-fire conditions and colonize new suitable thermal environments (Huey, 1991). This *a priori* positive response, however, is not homogeneous within a reptile assemblage, as habitat attributes and other environmental factors vary across the post-fire succession, favoring or harming species depending on their requirements (Rugiero and Luiselli 2006; Valentine and Schwarzkopf, 2008; Santos and Poquet, 2010), and promoting species-specific responses in reptiles within a single community (Driscoll and Henderson, 2008; Santos and Poquet, 2010).

In the context of a repeated fire regime, first we tested the intermediate disturbance hypothesis expecting higher reptile species richness in once burnt sites, and the most contrasted faunas between unburned and repeated burned transects. Response to fire has been extensively studied at a taxonomic level (e.g. in the Mediterranean basin by Moreira et al., 2001; Herrando et al., 2003; Brotons et al., 2008; Santos et al., 2009). More recently, several studies have examined the taxonomic response in parallel to the functional response of biota (Moretti and Legg, 2009; Mateos et al., 2011). This double approach provides information about taxonomic differences between burned and unburned areas and also about the mechanisms that drive community responses to environmental changes such as fire (Moretti et al., 2009). If repeated fires reduce plant diversity and increase abundance of xerophitic species (Pausas and Vallejo, 1999), we could expect a similar functional response in animal communities. If repeated fires favor plant species capable of rapid population recovery (Mouillot et al., 2003; Eugenio et al., 2006; Vilà-Cabrera et al., 2008), we could expect similar functional responses of animal species, favoring those with a short lifespan and a rapid population turnover. In this scenario, we have examined reptile functional responses to one and multiple fires according to their life-history traits as a partial approach to test the habitat accommodation model that predicts biotic positive responses according to specific habitat requirements.

2. Materials and methods

2.1. Study area and fire history

The study area was the Massif des Maures (Var, Provence region, southern France, 4°5″E /43°16″N; Fig. 1A). This is a vast coastal mountain chain with a surface area of around 1350 km^2 limited by the Mediterranean Sea (to the south), an agricultural plateau (to the north) and two rivers (to the east and west). The lithology of the massif is magmatic with a substrate composed of granite, gneiss and schist layers, in contrast to the calcareous layer of the rest of the region. The relief is abrupt, with several low-altitude chains (maximum altitude 780 m) oriented in a west–southwest to east–northeast direction along 60 km and crossed by permanent streams.

The study area has suffered very few disturbances apart from fire, in contrast to other nearby coastal areas that have been severely modified by humans. The vegetation consists of native forests, with oaks (*Quercus suber*, *Q. ilex*, *Q. pubescens*) and pines (*Pinus pinea*, *P. pinaster*, *P. halepensis*) making up the dominant tree species. Valleys around streams are occupied by deciduous forests (e.g. *Alnus glutinosa*, *Salix* spp., *Populus nigra*, *Fraxinus oxyphylla*). The most thermophilous sites are Mediterranean scrublands dominated by *Cistus* spp. *Arbustus unedo*, *Erica arborea* and *Myrtus communis*. The climate is Mediterranean, with an annual rainfall between 600 mm (on the coast) and 1200 mm (in the massif), annual sun exposure of 2880 h per year, and mild temperatures (mean minimum in January between 2 and 6 °C, mean maximum in July between 27 and 31 °C). The massif is partially protected by the French National Forest Office.

The study area is characterized by a high frequency of forest fires. We had access to fire-history mapping performed since 1958 by the *Direction Départementale de l'Agriculture et de la Forêt* (DDAF: Departmental Office of Agriculture and Forests) and the *Office National des Forêts* (ONF: French National Forest Office) in the Department of Var. During this 51-year period, 62.5% of the study area has burned at least once, 22.2% twice, and 13.5% three or more times. The spatial distribution of fires during this period was very heterogeneous: several zones in the center of the massif never burned, whereas others in the western and eastern parts burned up to six times with a fire frequency between consecutive fires averaging 10 years. Thus, the study area is a complex mosaic in terms of the number of fires, the frequency between consecutive fires, and the time elapsed since the last fire that occurred. This spatial distribution makes the Massif des Maures a natural laboratory to test the response of organisms to repeated fires.

2.2. Transect selection and sampling method

From April to June 2010, we sampled reptiles in 87 linear transects during sampling periods of 1 h per transect. Transects were carried out on sunny days during periods of maximum reptile activity. Each transect was sampled by one person walking slowly at a constant speed (average length per transect was 1.7 ± 0.05 km) and registering all visual reptile encounters. Given the transect length, this method allowed us to sample the habitat heterogeneity

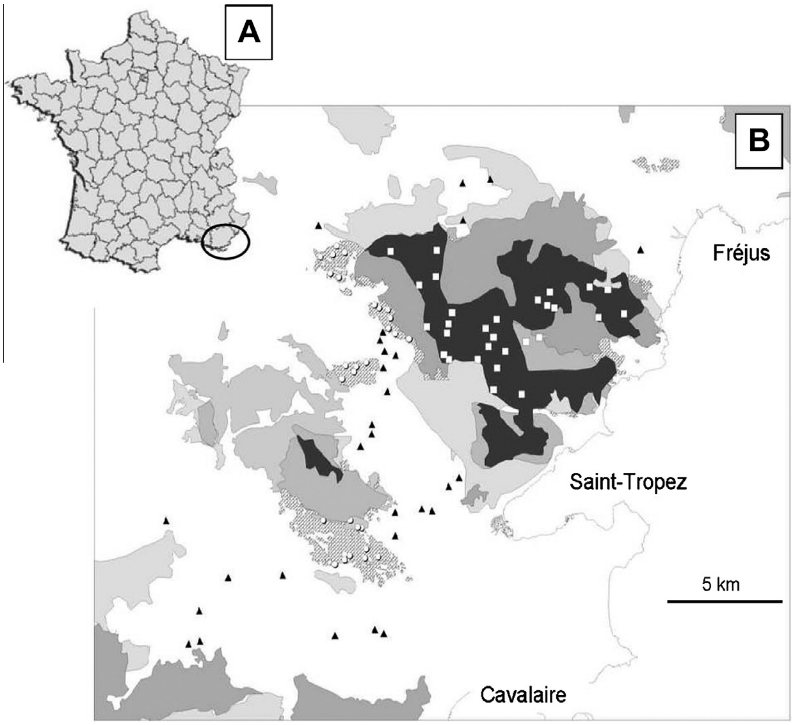

Fig. 1. Location of the Massif des Maures (Department of Var, southern France) (A) and distribution of transects according to the fire history of each polygon (B). Triangles: transects in areas never burned; circles: transects in areas only burned in 2003; squares: transects in areas burned three or more times. Grey range shows the number and year of fire: striped (only one fire in 2003); light grey (only one old fire in 1959, 1970 or 1979), dark grey (two fires); black (three or more fires, the last one in 2003).

within each fire regime by detecting active reptiles. For each sighting, we noted the species observed and its perpendicular distance to the line transect. Within the Massif des Maures, transects were carried out in three different fire regimes (29 replicates per regime, Fig. 1B) according to the following criteria: (1) Repeatedly burned areas (RBA), with 4–5 fires in the last 50 years, the last occurring in July 2003, and with an elapsed interval between consecutive fires averaging 10 years (Supplementary materials S1a); (2) Once-burned areas (OBA), burned in 2003 (Supplementary materials S1b); and (3) Unburned areas (UBA) that had not burned in the previous 51 years (Supplementary materials S1c). These criteria allowed us to avoid the potential effects of the time elapsed since the last fire, or the time between consecutive fires, both of which are factors already known to be important in the response of organisms to fire (Mouillot et al., 2003; Eugenio et al., 2006; Santos and Poquet, 2010). Within each fire regime, the start point of transects was determined randomly whereas the end point after 1 h sampling.

2.3. Methodological constraints and solutions

Before addressing the questions raised in the manuscript's objectives, we compared differences among the three fire-regime transects in altitude, slope, vegetation structure (before the fire), distance of reptile sightings, and spatial autocorrelation.

2.3.1. Orientation and altitude

Transects were carried out on south-facing slopes (between southwest and southeast) to avoid the potential effect of slope orientation in the composition of the reptile assemblage. The average altitude of transects was 201.3 ± 12.4 m (altitude range 46–538 m). There were differences in the average altitude of transects for different fire regimes, with UBA transects on average 100 m higher than OBA and RBA transects. According to this result, we have used altitude of transects as covariate in further multivariate analyses.

2.3.2. Vegetation structure

Reptiles are very sensitive to habitat structure: some species prefer open areas and others dense woodland canopy. Given the changes produced by fire, we quantitatively examined habitat structure before and after burning. Pre-fire habitat structure was analyzed by examining a set of aerial pictures from 1944 (14 years before the first big fire recorded at the study area) taken by the Allied forces (US and French) to prepare the invasion of France against the German army during the Second World War. These pictures were stored into the Photothèque d'Archéologie Méditerranéenne at the Centre Camille Jullian, Université Aix-Marseille, Maison de l'Homme et de la Méditerranée at Aix-en-Provence. After checking the quality of these images, we selected those located at our study area, digitalized, and georeferenced. Post-fire habitat structure was analyzed by examining a Google map aerial photograph from 2006 (i.e. three years after the last large fire in the study area). Transects were intersected to the 1944 and 2006 aerial pictures to examine several vegetation and groundcover variables at points spaced 50 m apart along transects. The pictures taken in 1944 do not cover all transects, but the 77% of them ($n = 67$), making possible to do a realistic comparison of changes in habitat structure between both periods (Supplementary materials S2). Vegetation variables included forest, forest edge, isolated trees (i.e. when tree stands were not in contact and canopy cover was not continuous), scrubland, and bare ground plus rocks. Based on Bray–Curtis similarity indices, pre- and post-fire habitat structure was compared between the three fire regimes using analysis of similarities (ANOSIM, PRIMER-E, 2001) and non-metric multidimensional scaling.

2.3.3. Distance of observation

We have calculated the mean distance at which reptiles were detected during each transect. An ANOVA test did not find significant differences among the three fire regimes in terms of the distance at which reptiles were detected during line transects

($F_{2,84} = 1.65$, $p = 0.2$). For the four commonest species, we calculated the mean distance at which specimens were detected during each transect; we did not find significant differences among the three fire regimes in the distance at which animals were detected: *Lacerta bilineata* $F_{2,52} = 1.40$, $p = 0.26$; *Podarcis muralis* $F_{2,40} = 0.14$, $p = 0.87$; *Tarentola mauritanica* $F_{2,33} = 3.03$, $p = 0.06$; *Timon lepidus* $F_{2,20} = 1.53$, $p = 0.24$. In other words, for each species, the distance of reptile detection was similar among fire regimes, indicating that the probability of encountering a species (i.e. a proxy of detectability) was independent of the three habitats sampled.

2.3.4. Spatial autocorrelation

OBA and RBA transects were spatially clustered (Fig. 1B) due to the criteria used for transect selection and the distribution of fires. For this reason, it was appropriate to test spatial autocorrelation in reptile composition among transects by means of a Mantel test. This tests the correlation between two or more matrices: in our case, the geographic distance matrix between pairs of transects (measured from the center of each transect) and the similarity matrix of reptile composition between pairs of transects. Distance and similarity matrices, as well as the Mantel test, were performed with the software Passage 1.1 (Rosenberg, 2004) within each fire regime. We did not find spatial autocorrelation in the reptile composition among unburned transects ($r = 0.06$, $p = 0.28$) but did among once-burned ($r = 0.17$, $p = 0.001$) and repeated-burned ($r = 0.29$, $p = 0.005$). According to these results, we have used latitude and longitude of transects as covariates in further multivariate analyses.

2.4. Functional traits

To analyze the functional response of reptiles to repeated fires, we selected four traits based on characteristics that are recognized as important in reptile autecology: (1) the preferred habitat (with three categories, namely, forests, semi-open areas for species living in ecotonal forest areas, and open areas); (2) the altitudinal range, based on the maximum and minimum altitudes recorded for each species in southern France (with three categories: namely, small <1000 m, medium 1000–2000 m, and large >2000 m), as this trait can reflect the ecological niche breadth of a species; (3) the dietary habits (with four categories: namely, herbivorous, insectivorous, terrestrial-vertebrate foragers, and amphibian foragers); (4) the age of sexual maturity of females (with three categories: namely, young $\leqslant 30$ months, medium 31–60 months, and old >61 - months from birth), which reflects the population turnover rate of a species. Functional traits of the species found along the transects is summarized in Table 1, taken from specific references in Salvador (http://www.vertebradosibericos.org/reptiles.html) and Böhme (1981–2005).

2.5. Statistical procedures

As a diversity index, we have calculated the effective numbers of species derived from the exponential of the Shannon–Wiener index, since the effective numbers of species produces a stable, easily interpreted, sensitive general similarity measure (Jost, 2006). Differences in reptile abundance and composition among transects were quantified by the Bray–Curtis similarity index which compares presence–absence and abundance of species between pairs of samples. From the Bray–Curtis similarity matrix of pairwise transect comparisons, differences in reptile composition and abundance among fire regimes was performed by ANOSIM (PRIMER-E, 2001). ANOSIM is a non-parametric tool to compare similarities in relative abundance of species between groups of samples (i.e. fire regimes), which gives a general R-value and further pairwise comparisons between fire regimes. R-values represent an estimate of the similarity in reptile composition and species abundance between fire regimes, and accordingly it is a measure of the spatial variability in community characteristics (i.e. beta diversity). The statistic R is based on the difference of mean ranks between groups and within groups. Thus, R scores are in the interval between -1 and +1, value 0 indicating completely random grouping. The statistical significance of observed R is assessed by permuting 999 times the grouping vector to obtain the empirical distribution of R under null-model.

The association between taxonomic and functional traits, and the three defined fire regimes were analyzed using the program CANOCO for Windows (version 4.55; ter Braak and Šmilauer, 2002). The unimodal or linear relation between variables and fire regimes was first tested by a Detrended Correspondence Analysis (DCA). According to ter Braak and Šmilauer (2002) and Lepš and Šmilauer (2003), a Canonical Correspondence Analysis (CCA) or a Redundancy Analysis (RDA) that assumes unimodal and linear distributions respectively should be applied when the length of the gradient (estimated with a DCA) is bigger or smaller than 4. Both CCA and RDA are ordination methods that represent the variation of a data matrix in a reduced number of dimensions. In both cases, we statistically analyzed the association between variables (species abundance) and the explanatory variable (fire regimes) by testing the relationship between the axes and variables by a permutation Monte Carlo test (ter Braak and Šmilauer, 2002). Taxonomic responses were analyzed with reptile-species abundances per transect. The functional response was assessed by calculating abundances of each category of functional trait per transect.

Table 1
Functional traits of species observed along transects. Each functional trait was divided in several functional categories (see Materials and Methods section). The altitudinal range and age of maturity are quantitative variables which were reclassified in classes.

	Habitat	Diet	Altitudinal range		Sexual maturity		Mediterraneity (% of area)
			Meters	Class	Months	Class	
TEHE	Semi-open	Herbivorous	650	1	138	3	100
LABI	Semi-open	Insectivorous	2057	3	20	1	20
ANFR	Forest	Insectivorous	2205	3	54	2	5
ZALO	Forest	Vertebrates	1400	2	60	2	10
NANA	Semi-open	Amphibians	2006	3	54	2	8
TAMA	Open	Insectivorous	678	1	16	1	100
TILE	Open	Insectivorous	1200	2	30	1	95
POMU	Semi-open	Insectivorous	2350	3	20	1	15
PSHI	Open	Insectivorous	1130	2	9	1	100
CHST	Open	Insectivorous	1350	2	20	1	100
MAMO	Semi-open	Vertebrates	1068	2	51	2	100
RHSC	Semi-open	Vertebrates	800	1	60	2	100

We performed diversity accumulation curves for the three areas studied. Curves were computed with *EstimateS* (Colwell, 2006), with the sample order randomized 50 times, replacing the sample computed each time. The program randomly selects a single sample from the set and computes diversity, then selects two samples and computes diversity, and so on until the pooled number of samples is the same as the full sample set (in our case, 29 samples). Each distinct randomization accumulates the samples in a different order, and then performs different diversity accumulation curves. By randomizing samples using replacement, the software calculates mean and variance for each sample order of the curve, and can thus be used to compare datasets (in our case, the three areas according to the number of fires). Diversity accumulation curves were built by the Chao1 metric which estimates total species richness. This index take into account the number of singletons (species captured once), and doubletons (species captured twice), and is particularly useful for data sets skewed toward low-abundance classes (Chao, 1984).

We also created a Mediterranean Index to determine how the reptiles observed in each transect fit into a strict Mediterranean community (see a similar application for birds in Prodon, 1993). The level of ‘Mediterraneity’ of a reptile species was assessed by the percentage of the overall distribution of the species (IUCN, 2010) that fell within the limits of the Mediterranean biome in the Palearctic (Quézel and Médail, 2003). Variation in the Mediterranean Index among fire regimes was tested by means of ANOVA tests. From the overall matrix of abundances of all reptile species, we carried out a Principal Component Analysis (PCA) to summarize the variability in reptile composition of transects in a reduced number of axes ordering the reptile species according to their affinity to repeatedly burned in contrast to unburned or once-burned regimes. The Mediterranean Index was finally correlated to the first PCA axis score for each species to check for a relation between the response of reptiles to fire and their level of Mediterraneity.

Variables were checked for normality and homoscedasticity of variances before parametric tests (e.g. ANOVA). Non-parametric tests (e.g. Kruskal–Wallis tests) were performed when variables did not meet the assumptions for parametric analysis.

3. Results

3.1. Changes in habitat structure

Based on the similarity matrix between transects using the Bray–Curtis Index, the ANOSIM analysis did not show overall significant differences (global $R = 0.078$, $P = 0.08$), nor significant differences in all pairwise comparisons (UBA vs. OBA, $R = 0.067$, $P = 0.5$; UBA vs. RBA, $R = 0.135$, $P = 0.08$; OBA vs. RBA, $R = 0.047$, $P = 1$) on the habitat structure measured in 1944 for the transects classified within the three fire regimes. In contrast, the ANOSIM showed strong overall and pairwise differences on the habitat structure measured in 2006 (overall $R = 0.729$, $P = 0.01$; UBA vs. OBA, $R = 0.959$, $P = 0.01$; UBA vs. RBA, $R = 0.991$, $P = 0.01$; OBA vs. RBA, $R = 0.198$, $P = 0.01$). The non-metric multidimensional scaling ordination showed the same differences (Supplementary materials S2). This result indicates that the fire regime along the 1944–2006 period modified the landscape from a rather homogeneous sparse forest (56% of the points) to a contrasted mixture of scrubland and dense forest.

3.2. Taxonomic response of the reptile assemblage

In the 87 transects surveyed, we found 315 reptiles of 12 species (Table 2). We observed significant differences in the number of reptiles seen per transect among the three fire regimes (Kruskal–Wallis test, $H_{2,87} = 5.85$, $p = 0.05$, Supplementary materials S3A), although we did not find differences in the number of species seen per transect (K–W test: $H_{2,87} = 0.37$, $p = 0.8$, Supplementary materials S3B) nor in the effective number of species seen per transect (K–W test: $H_{2,87} = 0.04$, $p = 0.98$).

Three lizard species (*Tarentola mauritanica*, *Podarcis muralis* and *Lacerta bilineata*) each represented around 25% of reptiles seen. However, we found great differences of relative abundances of species among fire regimes (Table 2), as some species tended to decrease with fires (*Lacerta bilineata* and *Testudo hermanni*), and others to increase (*Tarentola mauritanica* and *Timon lepidus*), with one species (*P. muralis*) particularly abundant after one fire.

Based on the similarity matrix between transects using the Bray–Curtis Index, the ANOSIM analysis showed overall significant differences ($R = 0.395$, $P = 0.001$), as well as significant differences in all pairwise comparisons (UBA vs. OBA, $R = 0.086$, $P = 0.006$; UBA vs. RBA, $R = 0.585$, $P = 0.001$; OBA vs. RBA, $R = 0.515$, $P = 0.001$). Thus, the biggest differences among fire regimes (beta diversity) were between RBA and the other two, although differences between UBA and OBA also existed.

The CCA using altitude, latitude and longitude as covariates also showed significant differences in species composition and abundance between fire regimes (trace = 0.35, *F*-ratio = 4.36, $P = 0.001$). The biggest differences were between unburned and burned regimes, with a significant discrimination in axis 1 (eigenvalue = 0.24, *F*-ratio = 5.82, $P = 0.001$) and association with *T. hermanni* and *L. bilineata* as the commonest species in UBA (Fig. 2). The second axis (eigenvalue = 0.11) discriminated between once-burned and repeated burned regimes with *T. mauritanica* and *T. lepidus* associated to repeated burned, and *P. muralis* to

Table 2
Relative abundance and percentage of the 12 species found in transects made in three types of fire regimes: unburned, once burned and repeatedly burned.

			0 Fires		1 Fire		N fires		Total	
Species			N	%	N	%	N	%	N	%
Testudo hermanni	TEHE	Turtle	10	11.76	4	3.42	0	0.00	14	4.44
Tarentola mauritanica	TAMA	Lizard	5	5.88	8	6.84	63	55.75	76	24.13
Podarcis muralis	POMU	“	18	21.18	54	46.15	7	6.19	79	25.08
Lacerta bilineata	LABI	“	40	47.06	34	29.06	12	10.62	86	27.30
Timon lepidus	TILE	“	1	1.18	6	5.13	23	20.35	30	9.52
Psammodromus hispanicus	PSHI	“	0	0.00	5	4.27	6	5.31	11	3.49
Anguis fragilis	ANFR	“	1	1.18	0	0.00	0	0.00	1	0.32
Chalcides striatus	CHST	“	0	0.00	0	0.00	1	0.88	1	0.32
Malpolon monspessulanus	MAMO	Snake	5	5.88	6	5.13	1	0.88	12	3.81
Rhinechis scalaris	RHSC	“	1	1.18	0	0.00	0	0.00	1	0.32
Zamenis longissimus	ZALO	“	2	2.35	0	0.00	0	0.00	2	0.63
Natrix natrix	NANA	“	2	2.35	0	0.00	0	0.00	2	0.63
	Total reptiles		85	117	113	315				
	Total species		10	7	7	12				

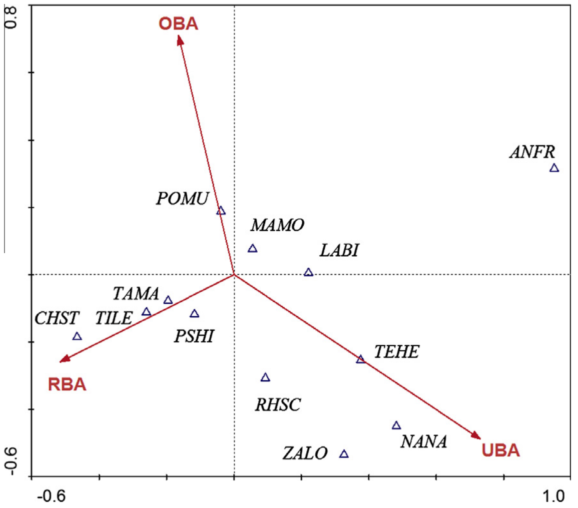

Fig. 2. Biplot of the Canonical Correspondence Analysis of the association between reptile species and fire regimes. Fire regimes: unburned (UBA), once burned (OBA), and repeatedly burned (RBA). See the meaning of reptile acronyms in Table 2.

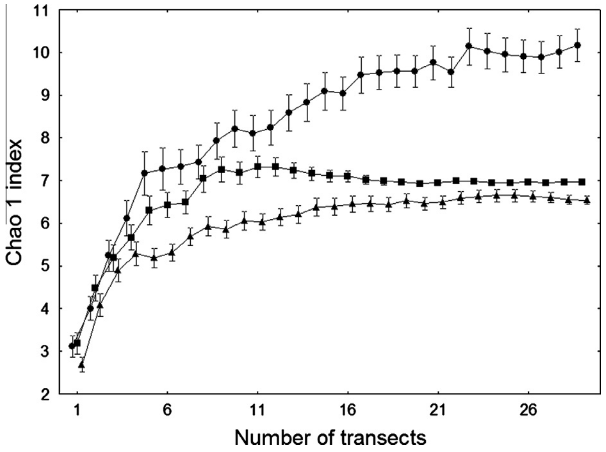

Fig. 3. Diversity accumulative curves according to fire regimes. Symbols represent the mean of 50 randomizations and whiskers ± SE. Circles: unburned (UBA), triangles: once burned (OBA), and diamonds: repeatedly burned (RBA).

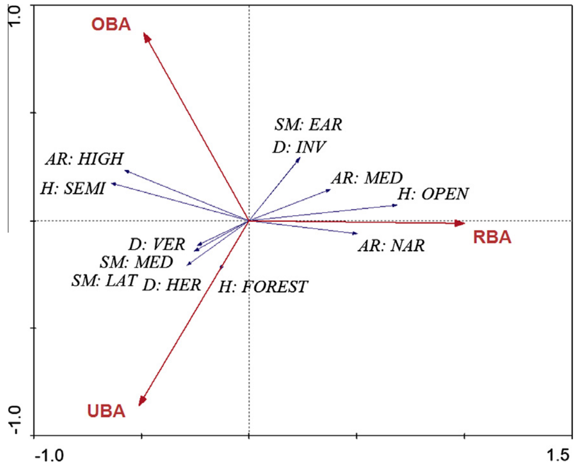

Fig. 4. Redundancy analysis plot of the association between functional traits and fire regimes. Fire regimes: unburned (UBA), once burned (OBA), and repeatedly burned (RBA). Functional traits and classes: altitude range (AR): high (HIGH), medium (MED) and narrow (NAR); sexual maturity (SM): early (EAR), medium (MED) and late (LAT); habitat (H): forest (FOREST), open areas (OPEN) and semi-open areas (SEMI); diet (D): herbivory (HER), invertebrate prey (INV) and vertebrate prey (VER).

once-burned regimes. Individually, the three covariates, i.e. altitude, latitude and longitude explained 10%, 28% and 20% of the explained variance in reptile abundances in transects.

The accumulative curves of diversity for the three areas fitted a logarithmic function (Fig. 3), indicating that the sampling method with 29 replicates per fire regime accounted for the total reptile diversity in the study area. More interestingly, each curve saturates at different diversity scores with low standard error intervals (Fig. 3), revealing a loss of reptile diversity with an increasing number of fires.

3.3. Functional response of the reptile assemblage

The RDA showed significant differences in the functional traits of reptiles among fire regimes (trace = 0.29, *F*-ratio = 17.23, *P* = 0.0001). The first axis significantly discriminated between RBA and the other two regimes, whereas the second axis, also significant, discriminated between UBA and OBA (Fig. 4). Functional traits associated with RBA were open-habitat species, with low and medium niche breadth, early sexual maturity and a diet of invertebrates. In the second axis, forest habitats, normal and delayed maturity, and an herbivorous and vertebrate diet were the functional traits associated with UBA (Fig. 4).

Species with the smallest proportion of their range within the Mediterranean ecoregion (e.g. *Lacerta bilineata* and *Podarcis muralis*) had the smallest scores on the first PCA axis (unburned transects); whereas Mediterranean species such as *Tarentola mauritanica* and *Timon lepidus* tended to have high PCA1 values (burned transects). The correlation between the Mediterranean index (i.e. the percentage of the species' distribution within the range of the Mediterranean ecoregion) and the first PCA axis scores ordering the reptile species according to their affinity to fire regimes, was not significant (Supplementary materials S4) probably because of the low sample size (*n* = 6 species), as rare species were excluded from this analysis.

4. Discussion

4.1. Taxonomic responses and changes in diversity with fire regimes

Our field-based study has demonstrated that the reptile assemblage responds both taxonomically and functionally to fire, with a small but significant response after one fire, and a more dramatic response after repeated fires. We found a general loss of diversity after one and multiple fires, and a clear replacement of dominant species for each fire regime. The loss of diversity after one fire does not support the intermediate disturbance hypothesis probably due to the severe effect of fire which reduce drastically canopy and harm species with particular habitat requirements. In a similar fieldwork design in a reptile assemblage from Australia, Lindenmayer et al. (2008) did not find evidences to support this hypothesis. These authors argued that the rapidity of post-fire recovery of many components of native vegetation limited opportunities for species associated to early post-fire conditions, hence precluding consistent results according to the habitat accommodation model of succession.

At a taxonomic level, we observed contrasting responses among fire regimes: some species decreased and others increased after repeated fires, while others showed maximum abundance in a regime of intermediate disturbance (once-burned areas). This uneven response to fire has been previously reported for other reptile communities (Driscoll and Henderson, 2008; Santos and Poquet, 2010; Driscoll et al., 2012) and is consistent with the high and also diversified dependence of these organisms to the changing vegetation structure during post-fire succession. Although we have removed the effect of the time since the last fire (last fire in 2003 in all burned areas), functional-trait replacement among fire regimes suggest that species accommodate to particular habitat requirements. Contrasted habitats linked to different fire regimes are probably maintained in the Massif des Maures due to a high fire frequency and a Mediterranean unpredictable rainfall that slows post-fire recovery.

4.2. Habitat transformation after fire and reptile functional responses

ANOSIM comparisons of the habitat structure in 1944 and 2006 indicated a strong association between habitats and transects in the post-fire situation, suggesting that the past 51 years of fires has increased the habitat contrast between the transects sampled. Although fires in the Maures were documented in the 18th and 19th centuries (Amouric, 1992), recent repeated-fire regimes have increased differences between unburned and burned areas as has occurred in other localities such as Corsica (Mouillot et al., 2003). Before the recent fire-regime, the landscape was dominated by a sparse forest. Currently, the unburned area is a mixed forest dominated by four tree species, *Quercus suber*, *Q. ilex*, *Q. pubescens* and *Pinus pinaster* with a dense canopy, whereas RBA transects are characterized by a homogeneous maquis of *Cistus* sp. and locally *Erica* sp. with a sparse occurrence of *Q. suber* stands (Supplementary materials S1) as this is the only tree in the study area capable to survive multiple fire events.

In addition, changes in habitat structure after repeated fires are expected to stress other components in the biota through bottom-up effects that can disturb species' interactions and constrain ecosystem functioning. The mechanisms that drive these processes can be studied in part by analyzing the functional response of organisms (Chapin et al., 2000). In this sense, the functional response of reptiles in the Massif des Maures indicates that after repeated fires, the reptile assemblage is composed of more specialized species (i.e. narrow altitudinal ranges), with shorter lifespans and insectivorous dietary habits. Moretti and Legg (2009) reported that fire acts as an environmental filter, selecting the traits most suitable to fire and post-fire conditions (e.g. fire results in selection for dispersal and pioneer-habitat traits in arthropods from southern Switzerland, Moretti and Legg, 2009). The functional response observed in Mediterranean reptiles supports this theory of the selection role of fire, as the environmental conditions in burned areas (more xerophilous and thermophilous habitats) are the underlying cause of the shifts in dominant species observed in repeated fire regimes.

Although thermal data for the species recorded in the Massif des Maures is heterogeneous (Supplementary materials S5), we detected that the commonest species in unburned transects have smaller thermal preferences and ranges than species of repeatedly burned habitats. At a local scale, the intensity of solar radiation and temperature of potential retreat sites increase with increasing canopy openness (Pringle et al., 2003). As repeated fires reduce canopy, microhabitat thermal regimes can be modified, and this factor may affect habitat quality of species with particularly narrow thermal niches (Webb et al., 2005). This mechanistic explanation of causes underlying species substitution across a fire gradient is in agreement that thermal quality of the environment can have significant physiological and behavioral costs (Huey, 1991). These costs could ultimately explain species replacement in the Massif des Maures after one and repeated fires.

Our results also support a functional response to repeated fire regimes. In these scenarios, the interval between successive fires plays a key role in the response of plant species, which can be measured by their resprouting ability and persistence capacity (Pausas et al., 2004). Mediterranean vegetation is considered to be resilient to fire (Blondel et al., 2010), although several studies have shown resprouting difficulties (Eugenio and Lloret, 2004) and decreasing resilience patterns (Díaz-Delgado et al., 2002) after repeated fires, since short inter-fire intervals prevent seedlings from growing and decrease seed-bank storage in the soil (Keeley et al., 1999; Eugenio et al., 2006). This process can promote the extent of species with a short lifespan (Lloret et al., 2003; Mouillot et al., 2003) in a similar way as fire promotes multivoltine bee species in Switzerland (Moretti et al., 2009) and encourages short-lifespan reptiles in southern France (our study). In structurally simple ecosystems such as savannahs and grasslands, the effects of repeated fire regimes can show positive responses in terms of diversity for some resilient groups (e.g. Orgeas and Andersen, 2001, but see Nekola, 2002). However, in complex ecosystems such as Mediterranean forests, it is clear that repeated fire regimes may have negative effects on slow-response organisms such as animals with a long lifespan.

4.3. Conservation remarks

The fact that overall reptile species richness is higher in unburned areas, while richness per transect did not differ among fire regimes indicates that there is a reduction in beta diversity from unburned to repeatedly burned plots. This implies that species composition among unburned transects differs at a higher degree than among once-burned and especially repeatedly burned transects. However, changes in dominant species from unburned to repeatedly burned areas might be an argument for maintaining a mosaic of areas burned at variable intervals. Mediterranean landscapes are recognized to have high habitat heterogeneity, in part maintained by a long fire history and co-existence of different land uses (Blondel et al., 2010). The landscape transformation produced by fire with the resulting increase of scrubland and open areas has been reported as a major agent for expansion of low-mobility animal groups (e.g. reptiles, Bury, 2004; Santos and Poquet, 2010) and high-mobility animal groups (e.g. birds, Moreira and Russo, 2007; Brotons et al., 2008). Our results are consistent with this trend, since differences in species presence and abundance between unburned and repeatedly burned transects were very large.

In a scenario of increasing fire risk and extension of fires, two spatial scenarios are possible: If fire occurrence is randomly distributed, then this repeated disturbance could result in a reduction of beta biodiversity. If fire affects the same places repeatedly, the result could be a contrasted mosaic of habitats promoting an increase of beta diversity at a regional scale. The distribution of fire over the last 50 years supports the second scenario in the Massif des Maures, as some areas are unaffected by fire, while others have been affected by more than six fires in the same period, a similar pattern observed in Corsica (Mouillot et al., 2003). The maintenance of this habitat heterogeneity with a mosaic of burned and unburned areas entails the application of fire exclusion policies in areas unburned since many years. For this reason, integrating cartography of fire history and areas of biological importance is needed in order to design fire management strategies. From a holistic (geographic) perspective, modeling the response of species in a scenario of contrasted fire regimes at a regional scale will be fundamental in designing conservation guidelines for the protection of particular habitats and species likely to be impacted by fire.

Our data suggests the continued loss of Hermann's tortoise under a scenario of expanding fire boundaries. This chelonian is listed as Near Threatened (NT) by the IUCN with a tendency towards a general population reduction (http://www.iucnredlist.org), especially the subspecies located in the western Mediterranean (including the Maures Massif) (Bertolero et al., 2011). This is a species with high conservation value, catalogued as endangered in France's Red List (UICN France, 2009). Habitat degradation and forest fires are recognized as main causes of tortoise mortality (Bertolero et al., 2011), with estimates of 50–85% of adults killed as a result of fire in the Massif des Maures (Cheylan, 1984; Couturier et al., 2011). The loss of traditional agricultural and livestock uses of the land and rising global temperatures are expected to increase the risk and frequency of fires, with a consequent increase of their destructive capability (Pausas and Keeley, 2009). This will in turn increase extinction risk within most of *T. hermanni*'s current range (Fernández-Chacón et al., 2011). In this scenario, areas with high tortoise density are being delimited and georeferenced (Cheylan et al., 2013) in order to prevent future fires as the best management practice to ensure the survival of the Maure's population.

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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.biocon.2013.09.008.

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