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CONTRIBUTED PAPER

Reptile responses to fire across the western Mediterranean Basin

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Abstract

Effects of anthropogenic activities, including climate change, are modifying fire regimes, and the dynamic nature of these modifications requires identification of general patterns of organisms' responses to fire. This is a challenging task because of the high complexity of factors involved (including climate, geography, land use, and species-specific ecology). We aimed to describe the responses of the reptile community to fire across a range of environmental and fire-history conditions in the western Mediterranean Basin. We sampled 8 sites that spanned 4 Mediterranean countries. We recorded 6064 reptile sightings of 36 species in 1620 transects and modeled 3 community metrics (total number of individuals, species richness, and Shannon diversity) as responses to environmental and fire-history variables. Reptile community composition was also analyzed. Habitat type (natural vs. afforestation), fire age class (time since the last fire), rainfall, and temperature were important factors in explaining these metrics. The total number of individuals varied according to fire age class, reaching a peak at 15–40 years after the last fire. Species richness and Shannon diversity were more stable during postfire years. The 3 community metrics were higher under postfire conditions than in unburned forest plots. This pattern was particularly prevalent in afforested plots, indicating that the negative effect of fire on reptiles was lower than the negative effect of afforestation. Community composition varied by fire age class, indicating the existence of early- and late-successional species (xeric and saxicolous vs. mesic reptiles, respectively). Species richness was 46% higher in areas with a single fire age class relative to those with a mixture of fire age classes, which indicates pyrodiverse landscapes promoted reptile diversity. An expected shift to more frequent fires will bias fire age distribution toward a predominance of early stages, and this will be harmful to reptile communities.

KEYWORDS
afforestation, fire, fire age class, land-use change, reptiles

INTRODUCTION

Fire shapes landscapes and the structure of animal communities in many regions worldwide (Kelly et al., 2020). Burned and unburned parts of the landscape tend to show different animal composition and diversity (Viljur et al., 2022). These differences can be driven by direct mortality caused by fire (Jolly et al., 2022); transformation of the habitat structure and microclimatic conditions from a closed (shady) environment to a more open postfire environment (Andersen, 2019; Bury, 2004; Lindenmayer et al., 2008; Valentine et al., 2012); and life-history traits that make some species more resistant or resilient to fire than others (Hu et al., 2016; Pausas, 2019; Santos et al., 2014). These factors drive changes in community composition from

pre- to postfire conditions and throughout postfire succession based on species' adaptive traits (Kelly et al., 2011; Santos et al., 2022; Senior et al., 2022; Smith, 2018).

In recent decades, rural abandonment and the associated increase in fuel loads, coupled with climate change, are increasing the size, frequency, season, and intensity of fires in many regions of the world (Moreira et al., 2011; Parisien et al., 2023; Pausas, 2022; Westerling, 2016), and this is threatening biodiversity (Kelly et al., 2020). Multiple studies have addressed the impacts of these changes by comparing plant or animal communities between unburned and burned areas. A wide array of taxonomic groups has been used as model organisms (reviewed by Viljur et al. (2022)). The last decade has been characterized by the publication of studies describing general responses of organisms to fire, classifying their functional postfire responses [Pausas, 2019), and identifying the life-history traits that make species vulnerable or resilient to fire (Chergui et al., 2020; Lindenmayer et al., 2008).

In the case of animals, meta-analyses show a diverse array of responses to fire that limits possible generalization (Appendix S1). Three factors can explain the lack of a general fire response trend: animals display a huge diversity of life-history traits to respond to fire (Pausas & Parr, 2018); animals are mobile and their responses are often behavioral and difficult to depict (Pausas, 2019); and abiotic conditions during fire are spatially and temporally variable, making animal responses highly dependent from the local context (Nimmo et al., 2014; Whelan, 1995).

In addition to fire, other environmental factors, such as habitat type and climate, can covary with fire variables to shape the animal communities at a regional scale (Nimmo et al., 2014). This is especially relevant for ectothermic organisms, such as reptiles, because their distribution patterns are strongly shaped by climatic features (Ficetola et al., 2013); their physiology makes them very sensitive to environmental changes (Huey, 1982), such as those promoted by habitat openness after fire; and their small home range is typically smaller than the fire size (Perry & Garland, 2002). Therefore, a comprehensive understanding of the impact of fire on reptile assemblages in fire-prone regions requires the consideration of a suite of fire-history and environmental factors.

We aimed to gain insights into the fire–reptile relationship at a broad geographic scale. Thus, we focused on a region with similar fire regime and climate features but variable environmental and fire-history conditions in the region, specifically, the western Mediterranean Basin, a fire-prone region that encompasses a range of environmental conditions and land uses (including afforestation, a widespread land use in the region) that are expected to shape reptile community composition and diversity. We examined reptile responses to wildfires that mostly occurred in summer during the dry and hot season across the western Mediterranean. Through field surveys, we measured total number of individuals (a surrogate of reptile abundance), species richness, Shannon diversity (i.e., a combination of species richness and species-specific abundances), and community composition. We made 3 primary predictions. First, we expected our metrics to increase in relatively wetter and warmer areas. Reptiles are ectotherms; thus, climate has a direct influence on species distributions (Aragón et al., 2010) and population demography (Lazzari et al., 2022). At the geographic scale, reptile richness increases at relatively lower latitudes and higher temperature (Whiting & Fox, 2021).

Second, we expected the total number of individuals, species richness, and Shannon diversity of reptiles postfire to follow vegetation cover—that is, we expected a decline after a fire and a return to the prefire state as succession progressed postfire (i.e., correlation with time since fire). There is evidence of the abrupt decline in the total number of individuals 1 year postfire at the local scale (Santos et al., 2016, 2022) and of the postfire recovery depending on the vegetation recovery (Lindenmayer et al., 2008).

Third, we predicted that forests dominated by native (mainly broad-leaved) tree species would hold more complex reptile communities (i.e., more individuals, species, and higher Shannon diversity) than tree plantations (mostly pine monocultures). Native forests are more complex in terms of habitat structure and plant diversity (Brockerhoff et al., 2008) and thus provide more microhabitat heterogeneity to support a richer reptile community than plantations (Pinto et al., 2018). Moreover, afforested stands typically have a high tree density, resulting in reduced ground-level radiation, which generates a suboptimal thermal environment for reptiles (Azor et al., 2015).

METHODS

Western Mediterranean Basin

The western Mediterranean region is a major hotspot of biodiversity largely due to its high rate of endemicity (Myers et al., 2000). It is located between the Arid and Atlantic ecoregions and has a hotter and drier climate toward the south and east (Ceballos et al., 2004). The Mediterranean region is characterized by high fire activity in summer (Keeley et al., 2012). In the last few decades, fires have been more intense and frequent (Moreira et al., 2011; Pausas, 2022; Pausas & Fernández-Muñoz, 2012). Fire shapes the habitat structure of Mediterranean landscapes (Keeley et al., 2012). Fire-adapted shrubs and trees dominate the area, and they have 2 major strategies to respond to fire: resprouting and seeding (Pausas & Keeley, 2014). Forests of the region are basically differentiated between broad-leaved forests dominated by native resprouting species (e.g., *Quercus* species) (Pausas, 2001) and pine woodlands, often planted with native or non-native species.

Study design

We surveyed 8 sites between 32° and 42° N latitude in 4 countries in the western part of the Mediterranean Basin (France, Spain, Portugal, and Morocco) (Figure 1). Sites covered a range of environmental conditions (habitat type and climate [Appendix S2]). Each site was selected based on its fire history (number of fires) and occurrence of fires in different years

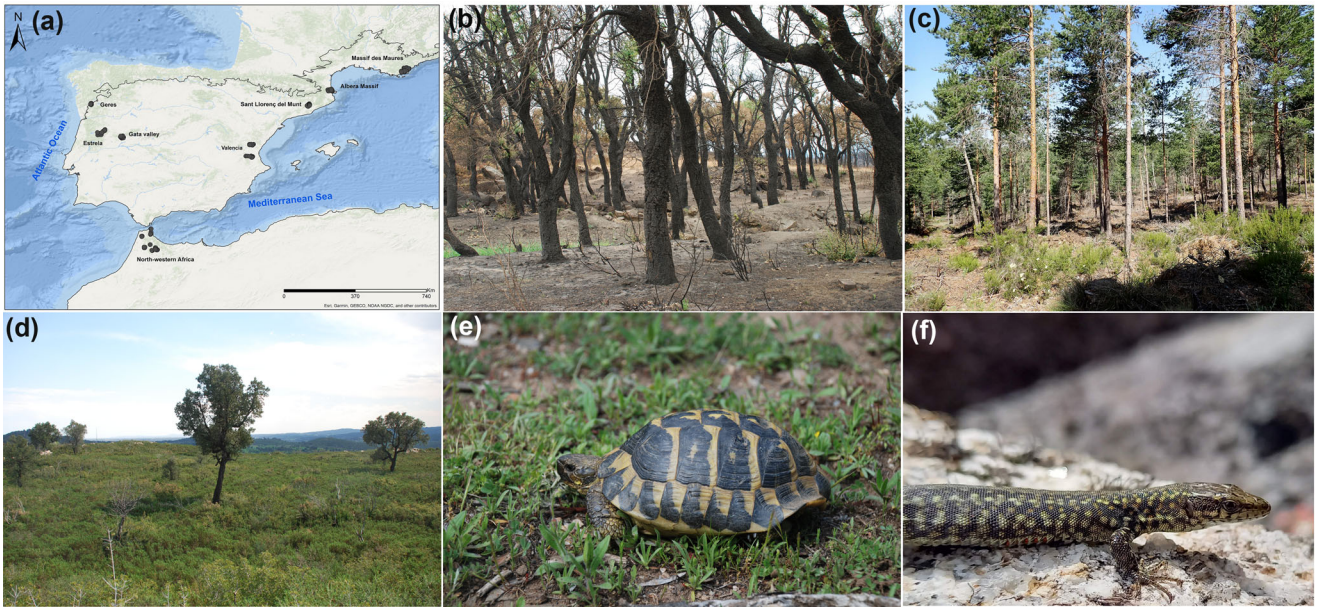

FIGURE 1 (a) Location of study sites ($n = 8$) in the western Mediterranean Basin (black line, northern limit of the Mediterranean climate zone); (b–d) habitats sampled for reptiles ([b] recently burned cork oak site in Albera; [c] long unburned afforested site at Gata valley, and [d] recurrently burned cork oak site in Maures); and (e, f) species detected in transects ([e] *Testudo hermanni* in Albera and [f] *Podarcis lusitanicus* in northern Portugal).

(fire age classes). We defined a site as an area (or landscape) with similar climatic and lithology features composed of a mixture of forest patches (native and afforested, burned and long unburned) and agricultural fields. Each site may include a range of patches with different postfire ages. Fires were usually located in mountainous forested areas, whereas agricultural fields were mostly distributed in valleys on flat areas.

Reptiles were sampled in burned plots affected by wildfires. None of the sites were managed with prescribed fires. Wildfires across the Mediterranean Basin usually occur in summer during the dry season. The sampling sites were selected in burned forested areas affected by high-intensity (crown) fires, which are the dominant fire type in the region (Keeley et al., 2012). Geographic variation in other fire-history features (e.g., recurrence and size of fires) was mostly associated with differences in socioeconomic and climatic factors in the Mediterranean (Chergui, Fahd, Santos, & Pausas, 2018).

In each site, we selected 5–61 plots with different fire age classes (363 plots) (Appendix S2). Plot was defined as a polygon approximately 25 × 1000 m with similar vegetation structure and fire history and the same dominant tree species. Each plot was characterized by 2 fire-history variables according to the available information: number of fires (usually in the last 40 years due to the lack of accurate spatial information before this period) and fire age class (years since the last fire). The number of fires varied from 0 to 6 fires, and time since the last fire ranged from 1 to >40 years. In our study sites, there was a gap of plots between 14 and 19 years since the last fire (Appendix S3). Moreover, there were no precise spatial fire-history information in many sites for fires older than 40 years (e.g., before 1975 in Portugal and before 1995 in Morocco). Due to these sampling constraints, we considered 3 fire age classes: early (<15 years postfire) (206 plots), middle (from 15 to 40 years postfire) (36 plots), and unburned (more than 40 years postfire) (121 plots) (Appendix S2). Each site included early plots and middle or unburned plots, or both middle and unburned plots, depending on their fire histories. In each site, all fire age plots had similar elevation, orientation, soil, and prefire vegetation. The middle and unburned plots were located as close as possible to early plots (average distance 1428 m [SE 252.7]), and average distance among early plots in the same fire perimeter was 1865 m (SE 480).

The fire-history variables were obtained from several sources, depending on the site and country: Departament d'Agricultura of Generalitat de Catalunya (for Albera Massif, Spain); Instituto da Conservação da Natureza e Florestas (for Serra da Estrela and Gerês, Portugal); Direction Départementale de l'Agriculture et de la Forêt and the Office National des Forêts (for Massif des Maures, France); and Direction Régionale de l'Agence Nationale des Eaux et Forêts Tanger-Tétouan-Al Hoceima (for Rif, Morocco).

Environmental variables

Three environmental variables were compiled for each plot: prefire habitat type (natural or afforestation), mean annual rainfall, and mean annual temperature. We designated as natural those plots dominated by native broad-leaved resprouting trees (mainly oak species) (details in Appendix S4) with no evidence of being planted (although they may be managed) (Appendix S4). By afforestation, we refer to plantations of nonresprouting pines (native or introduced). Early afforested plots were composed of scrubland with some young pines and were classified as

afforested habitats according to their prefire composition. From the 363 plots, 207 were in natural-type habitats (116 in early, 24 in middle, and 67 in unburned fire age classes), and 156 were in afforested-type habitats (90 in early, 12 in middle, and 54 in unburned fire age classes).

Mean monthly climatic data (rainfall and temperature) for 1970–2000 were extracted from WorldClim (version 2.1; spatial resolution of 30 arc seconds) (Abatzoglou et al., 2018; Fick & Hijmans, 2017). Climatic data were obtained by intersecting the pixels and plots for reptile sampling. Maps from each plot were clipped, cropped, projected, and resampled using the Spatial Analyst extension of ArcGIS (ArcMap 10.4, Esri).

Reptile sampling

Reptiles were sampled in all plots through linear transects (the unit of sampling and analysis) during the reproductive season (April to June), when reptile activity is high in the Mediterranean Basin. Transects were situated along paths and narrow unpaved roads to increase reptile detectability. Except in one site (Maures, southern France), each plot was sampled 3–8 times (separated by at least 2 weeks) across all sampling years. Thus, the total number of transects in the 363 plots was 1624 (details in Appendix S2). *Transect* hereafter refers to a sampling event carried out along a plot during a specific date. All the transects at each site had a fixed duration, which ranged among sites from 30 min (in one site), to 45 min (in 4 sites), to 1 h (in 3 sites). Reptile sampling methodology was the same in the 8 sites (details below). Transect duration was used to control the sampling effort for statistical analysis, and the length of the transect at each site was similar (e.g., 0.98 km [SE 0.54] for 45 min and 1.41 km [SE 0.57] for 60 min of sampling). Each transect was surveyed by a single researcher, mainly X.S. (55% of transects). Local herpetologists and trained students surveyed the remaining transects.

Reptiles were visually sampled as the researcher walked slowly along the transect and actively searched in vegetation, rocks, and other refuges in the transect (described in Santos & Cheylan [2013] and Santos et al. [2016]). Sampling was performed during sunny and windless days (temperature range 20–30°C). Reptile specimens were identified to species level, with a few exceptions that were considered only for modeling the total number of individuals per transect. Sex and adult–nonadult categories were also recorded when possible.

Reptile detectability varies with the complexity of the vegetation structure (Couturier et al., 2014). However, for most species, differences in the distance of detection between early and middle-unburned plots (Santos & Cheylan, 2013; Santos et al., 2016) were not observed. The only exception was *Testudo graeca* from the Rif (Chergui et al., 2019), although the low number of sights for this species precludes bias on the metrics we analyzed. Thus, we did not apply a population correction to our data by fire age class.

Data analyses

We used the transect sampled in a plot and date as the sampling unit. From each transect, we obtained total number of individuals, species richness (number of different reptile species), and Shannon diversity; these metrics were used as dependent variables in further analyses.

We first evaluated the collinearity among the predictor variables by computing the variance inflation factor (VIF) with the function check_collinearity in the performance package (Lüdecke et al., 2021). The VIF was always <2, indicating that explanatory variables had independent information and therefore did not lead to biased estimation (Yoo et al., 2014). Then, we standardized (i.e., centered and scaled) all continuous predictors prior to analyses. We built generalized linear mixed models (GLMMs) with the glmmTMB package 1.1.8 (Brooks et al., 2017) to fit species richness and Shannon diversity against 5 independent predictors: 3 environmental (habitat type, mean annual rainfall, and mean annual temperature) and 2 fire-history variables (fire age class and number of fires) (Table 1). The interaction between fire age class and habitat type was also tested. A zero-inflated Poisson distribution was assumed for species richness because it takes into consideration overdispersion (in part due to the number of transects without reptile sights). Shannon diversity was modeled with a Gaussian distribution.

The use of classic Poisson regression and negative binomial models does not adequately address overdispersion when count data have many zeros (as in our case). Therefore, we used Hurdle regressions to model total number of individuals, which are adequate to deal with these particular data sets. This procedure has 2 components: a binomial model that assesses the probability of attaining a value of 0 (i.e., no reptile sights in a transect) and a truncated Poisson distribution for positive observations (i.e., transects with reptile sights). Hurdle regression models were also performed with the glmmTMB package (Brooks et al., 2017).

In all models, to account for sampling design (the different duration of the transects), site was used as a random factor. To account for repeated sampling (i.e., several transects in the same plot within and during several years), we added transect code nested within site as a random factor.

We assessed the magnitude (effect size) and ecological meaning (positive or negative) of predictors by showing model coefficients and 95% coefficient intervals. Confidence intervals not overlapping 0 indicated a significant effect ($p < 0.05$). Marginal and conditional R^2 values (mR^2 and cR^2, including only fixed and random + fixed effects, respectively) were calculated for each model to asses model fit and robustness with the function r.squaredGLMM from the package MuMIn (Barton, 2018). The quantile (Q–Q) plot of model residuals and predicted values was checked on each model to confirm normality of residuals with the DHARMa package in R (Hartig & Lohse, 2022).

TABLE 1 Environmental and fire-history variables used to model reptile community metrics (abundance, species richness, and Shannon diversity) in the western Mediterranean Basin with general linear mixed models and general additive models.

Variable name	Variable type	Units or classes	Description
Fire age classes	Categorical	Early, middle, unburned	Last fire occurrence <15 years ago, 15–40 years ago, >40 years ago
Time since fire	Continuous	Number	Number of years since the last fire (only for early fire age class)
Number of fires	Continuous	Number	Number of fires in the last 50 years
Habitat type	Categorical	Natural or forested	Habitat type sampled in plots
Rainfall	Continuous	mm	Total annual precipitation (average value in the period 1970–2000)
Temperature	Continuous	°C	Annual mean temperature (average value in the period 1970–2000)

The ground-dwelling lizard *Psammodromus algirus* accounted for 50% of all sightings. Thus, we modeled its abundance following the same statistical procedure as for the total number of individuals (i.e., Hurdle regression models). The distribution range of this lizard included all the sampling sites except the Massif des Maures (southern France), so this site was excluded from the *P. algirus* model.

Additionally, to better understand the role of the first postfire years on total number of individuals, we used the transects in early plots (1–14 years since the last fire) to perform a quantitative analysis with generalized additive mixed models (GAMMs). This procedure aimed to model total number of individuals in response to years since the last fire, temperature, rainfall, and habitat type. A GAMM is a nonparametric method particularly useful for modeling nonlinear relationships, such as those between community metrics and time since fire (Kelly et al., 2011). As for the GLMM, site and transect code nested within site were used as random factors. We modeled total number of individuals with early plots excluding transects with 0 sights. The GAMMs had a Poisson error distribution, and the smooth term of the variable time since fire was held at $k = 10$ on the basis of better model fit estimated by Akaike information criterion (AIC) values.

For the whole data set, and for each separated sampled site, species-specific abundances of each transect were compared among the 3 fire age classes and between natural and afforested habitat types (when both occurred at the same site) with permutational multivariate analysis of variance (PERMANOVA) with the function adonis in the R package vegan (Oksanen et al., 2015). Pairwise similarity in species composition among transects was assessed using the Bray–Curtis similarity distance for species abundance data, and the Jaccard similarity index was used for occurrence (species presence or absence) data. We used 999 permutations to fit PERMANOVA models with main effects of fire age class and habitat type and the interaction of both factors. Site and transect code (for overall) and transect code (for each of the 8 sites) were used as random effects.

To explore which species explained differences in species composition among fire age classes, we performed a redundancy analysis (RDA) with the vegan package (Oksanen et al., 2015). The RDA allowed us to identify the association between species abundances and fire age classes. The significance of the explained variance in the RDA was calculated by performing analysis-of-variance-like 9999 permutation tests.

We checked whether the number of species was greater at more pyrodiverse landscapes (i.e., landscapes with a mixture of fire age plots). For this purpose, we counted the total number of species found at each fire age class and site, the number of species found in a combination of pairs of fire age classes (early + middle, middle + unburned, early + unburned), and the number of species found in all fire age classes together at each site. These values were modeled with a GLMM that included scaled mean annual temperature and rainfall for each site and site as a random effect. To control for the effect of increased number of species found when more plots were sampled, we constructed species accumulation curves to check how many transects were necessary to stabilize the number of species found (see a similar application in Santos et al. [2022]). All statistical analyses were carried out in the R Statistical Environment (R Core Team, 2021).

RESULTS

Species

We observed 6064 reptiles of 36 species in 1624 transects (Appendix S5): 3 chelonians, 2 amphisbaenians, 21 lizards, and 10 snake species. Lizards were the most common group of species (5755 sights, 94.9%), and the ground-dwelling lizard *P. algirus* was the most abundant species, accounting for 50% of all sightings. Some of the species were found in only one of the fire age classes, and all of them were rare in the sites where they were found. Specifically, the snakes *Natrix astreptophora*, *Natrix helvetica*, and *Zamenis longissimus* were exclusively detected in unburned plots, the chelonian *Mauremys leprosa* in middle plots, and the lizards *Chalcides colosii* and *Podarcis carbonelli* in early plots (Appendix S5). Five of the observed species (14%) were threatened (2 species endangered, 3 species vulnerable) and 4 (11%) were near threatened (https://www.iucnredlist.org/; accessed 4 May 2023) (Appendix S5).

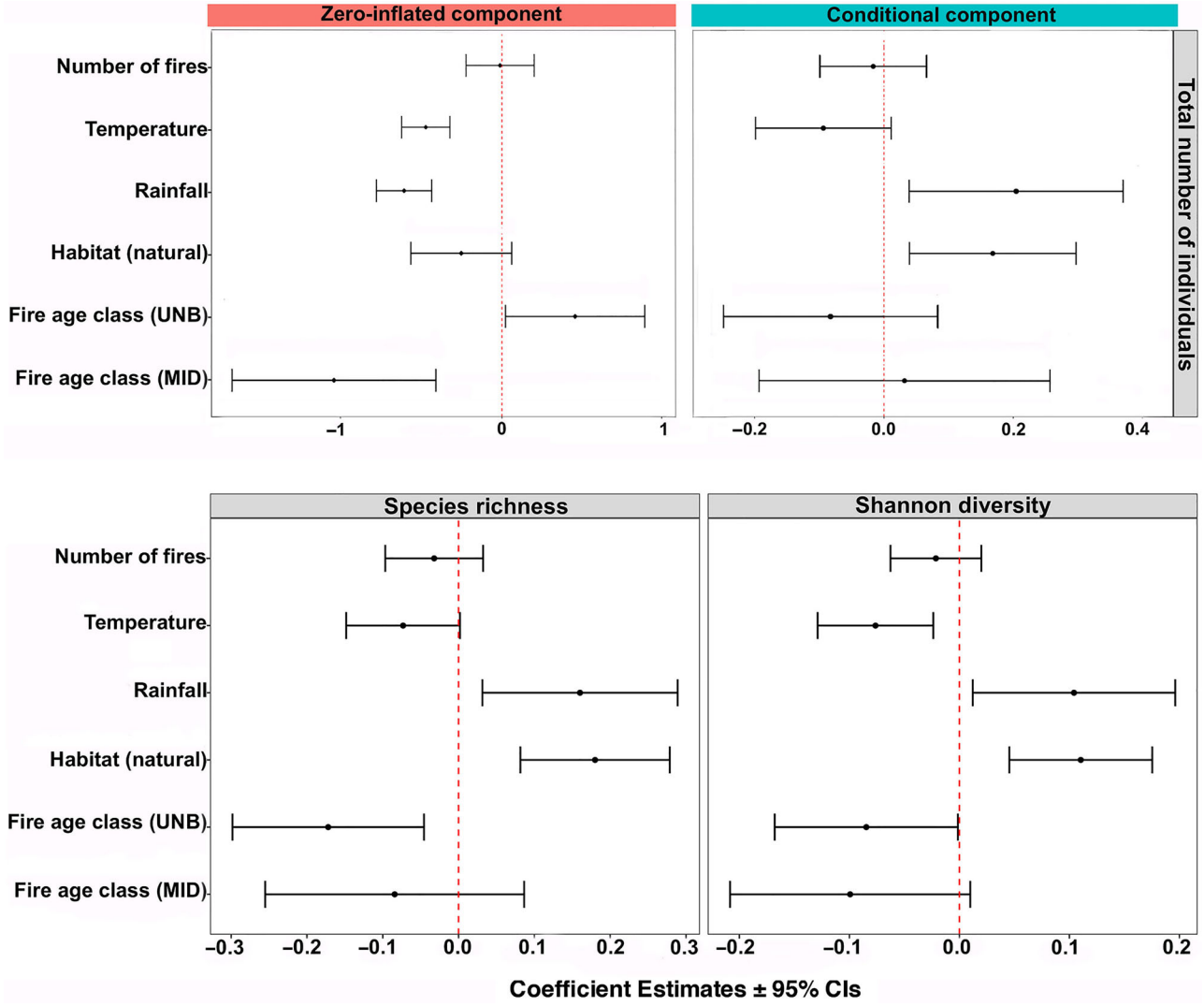

FIGURE 2 Estimated model coefficients and 95% confidence intervals (CIs) of the predictors used to model reptile total abundance of individuals, species richness, and Shannon diversity per transect. Predictor variables had a significant effect when 95% confidence interval did not overlap 0. Unburned (UNB) and middle (MID) fire age classes (defined in Table 1) are compared with the early fire age class. Total number of individuals was modeled with Hurdle regression models with 2 components: zero-inflated model and conditional model.

Community metrics and *P. algirus* abundance

The zero-inflated component of the Hurdle regression model for the total number of individuals showed that unburned plots had a higher probability of nondetection of any reptile (21.2% of transects) than early plots (17.5%), although middle plots showed the lowest probability of nondetection (5.6%). Moreover, temperature and rainfall increased the probability of detecting reptiles (Figure 2; Appendix S6). The conditional component showed that reptiles were more abundant in natural than in afforested plots regardless of the fire age class (Figure 2; Appendix S7). The total number of individuals increased as rainfall increased (Figure 2).

Four variables (habitat type, fire age class, rainfall, and temperature) were key explanatory variables for species richness (Figure 2; Appendix S6). Similar to the total number of individuals, species richness was higher in natural than in afforested plots regardless of fire age class and declined in unburned plots (Appendix S7). Species richness also increased as rainfall increased and decreased as temperature decreased (Figure 2).

Four variables (habitat type, fire age class, rainfall, and temperature) were important in explaining the Shannon diversity (Figure 2; Appendix S6). Natural plots had higher Shannon diversity than afforested plots, and this metric decreased in unburned compared with early plots. Shannon diversity also decreased as the mean annual temperature increased and decreased as rainfall increased (Figure 2).

The zero-inflated component of the Hurdle regression model showed that the presence of *P. algirus* was more probable in middle than early plots (86.4% and 64.5%, respectively) and in natural than in afforested plots (75.3% and 63%, respectively) (Figure 3). This lizard was found more frequently in plots with high temperature and rainfall and in plots with high fire recurrence (Figure 3). According to the conditional model, the

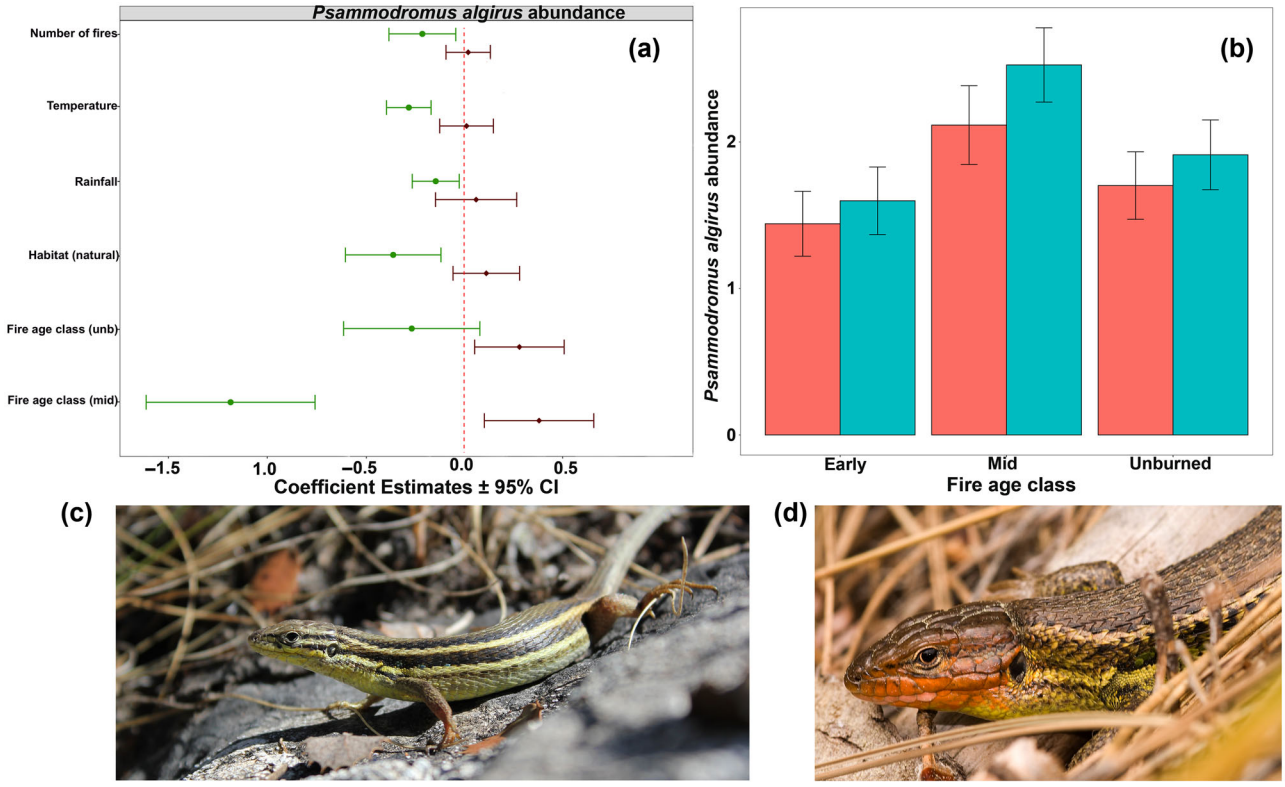

FIGURE 3 (a) Estimated model coefficients and 95% confidence intervals (CIs) of the predictors used to model *Psammodromus algirus* abundance per transect (modeled with Hurdle regression models with 2 components: zero-inflated model [green] and conditional model [red]), (b) effect of fire age class and habitat type (green, natural vegetation; red, afforestation) on *P. algirus* abundance (bars, mean estimates; whiskers, SE), (c) female *P. algirus* form the Rif, Morocco, and (d) head of a male from Ávila, Spain.

abundance of *P. algirus* was greater in middle and unburned plots than in early plots (Figure 3; Appendix S8).

Temporal variation during 14 postfire years

The total number of individuals seen per transect increased throughout the 14-year postfire period in both natural and afforested plots (effective degrees of freedom [edf] = 4.30, $F = 2.775$, $p = 0.03$ and edf = 1.00, $F = 4.712$, $p = 0.03$, respectively). Based on the GAMM prediction, the total number of individuals increased by 110% in natural plots and 54% in afforested plots from the first to the 14th year since fire. The total number of individuals per transect was higher in natural than afforested plots, except in recently burned plots (<6 years postfire), where the 95% confidence intervals overlapped greatly (Figure 4). The total number of individuals found in early plots also increased as rainfall increased ($p = 0.03$) and when temperatures reached 13°C ($p = 0.05$).

Community composition

The PERMANOVA analyses showed that reptile communities differed among fire age classes, habitat types, and the interaction between both factors (Table 2). These differences were driven by differences in species-specific abundances (overall and in all sites separately) and in the species occurrence (overall and in 5 sites) among early, middle, and unburned plots. In some sites, habitat type was also associated with differences in the community composition in both species-specific abundances and occurrence (Table 2).

The redundancy analyses showed a significant association of particular reptile species and fire age classes (variance = 0.175; df = 2; $F = 4.048$, $p = 0.001$). The first axis (RDA1 variance = 0.107; $F = 4.942$, $p = 0.001$) discriminated between unburned and early or middle plots, whereas the second axis (RDA2 variance = 0.068; $F = 3.153$, $p = 0.001$) discriminated between early and middle plots. We found an association of some Mediterranean and saxicolous lizards with early plots (e.g., *Tarentola mauritanica*, *Podarcis liolepis*, *Podarcis muralis*, *Psammodromus edwarsianus*) (Figure 5a). European and Atlantic species, such as *Zamenis longissimus*, *Natrix helveticus*, and *Lacerta schreiberi*, and the Mediterranean lizard *P. algirus* were associated with unburned plots. A European species (*Anguis fragilis*) and the Mediterranean tortoise (*Testudo hermanni*) were associated with middle plots (Figure 5a).

The number of species found in each fire age class and site averaged 8.14 species (early 9.21 species, middle 6.53, and unburned 8.67), and the average number of species found in sites with a mixture of the 3 fire age classes was 11.92 species (Figure 5b). From single to a combination of fire age classes, the number of species found increased 46.44%, and the GLMM

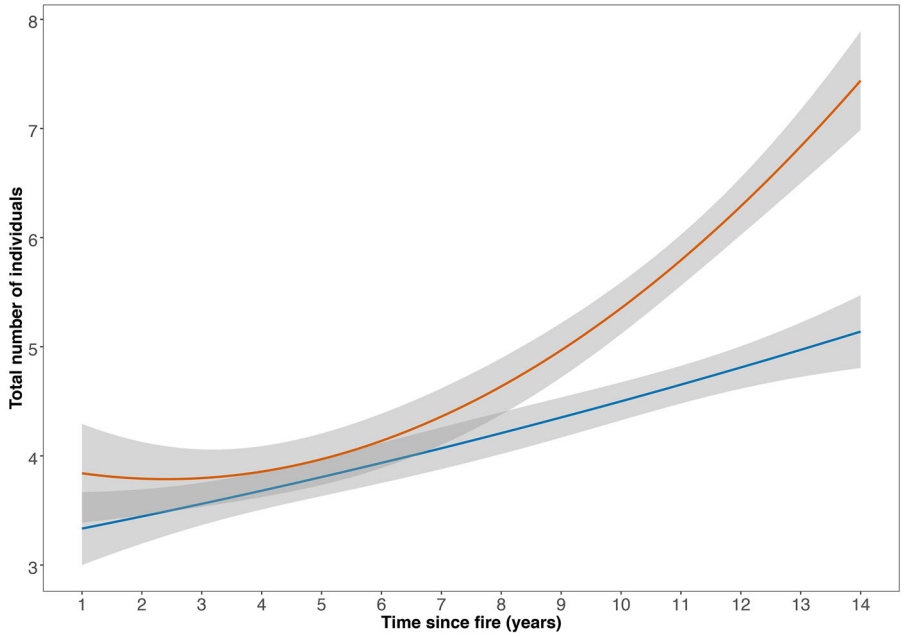

FIGURE 4 Response of total number of reptile individuals per transect to 14 postfire years since the last fire (line, fitted values from generalized additive mixed models; red, natural plots; blue, afforested plots; gray shading, 95% confidence intervals).

TABLE 2 Results of comparisons of the reptile community composition according to fire age class (early, middle, unburned [defined in Table 1]) and habitat type (natural and afforested) and its interaction in the overall data set and by site in the western Mediterranean.

		Abundance			Occurrence		
Site	**Factor**	***F***	***R*²**	***p***	***F***	***R*²**	***p***
Overall	Fire age class (FAC)	63.107	0.070	0.001	63.653	0.070	0.001
	Habitat type (HT)	22.986	0.013	0.001	36.050	0.019	0.001
	FAC × HT	11.399	0.012	0.001	15.081	0.016	0.001
Albera	FAC	14.056	0.082	0.001	9.851	0.059	0.001
	HT	0.356	0.002	0.836	0.199	0.001	0.909
	FAC × HT	2.363	0.014	0.056	1.581	0.009	0.192
Estrela	FAC	2.904	0.037	0.005	3.296	0.043	0.009
	HT	1.513	0.009	0.204	0.762	0.005	0.515
	FAC × HT	4.465	0.057	0.001	3.475	0.045	0.006
Gata	FAC	3.182	0.028	0.018	1.669	0.014	0.128
	HT	2.057	0.018	0.083	5.103	0.044	0.001
	FAC × HT	0.336	0.003	0.878	1.452	0.013	0.150
Gerês	FAC	2.804	0.068	0.005	1.507	0.037	0.183
Maures	FAC	10.206	0.107	0.001	9.108	0.097	0.001
	FAC	3.507	0.009	0.007	3.295	0.008	0.013
Rif	HT	7.926	0.021	0.001	10.662	0.027	0.001
	FAC × HT	0.626	0.002	0.711	0.642	0.002	0.665
	FAC	9.718	0.089	0.001	11.267	0.102	0.001
St. Llorenç	HT	6.818	0.031	0.002	8.587	0.039	0.002
	FAC × HT	2.387	0.022	0.057	1.667	0.015	0.163
Valencia	FAC	10.921	0.053	0.001	2.269	0.012	0.068

Note: Relative abundances of the species were compared using the Bray–Curtis similarity index, whereas species occurrence (presence or absence) was compared with the Jaccard index. Habitat type was not considered when only one type was sampled at a single site (i.e., at Gerês, Maures, and Valencia).

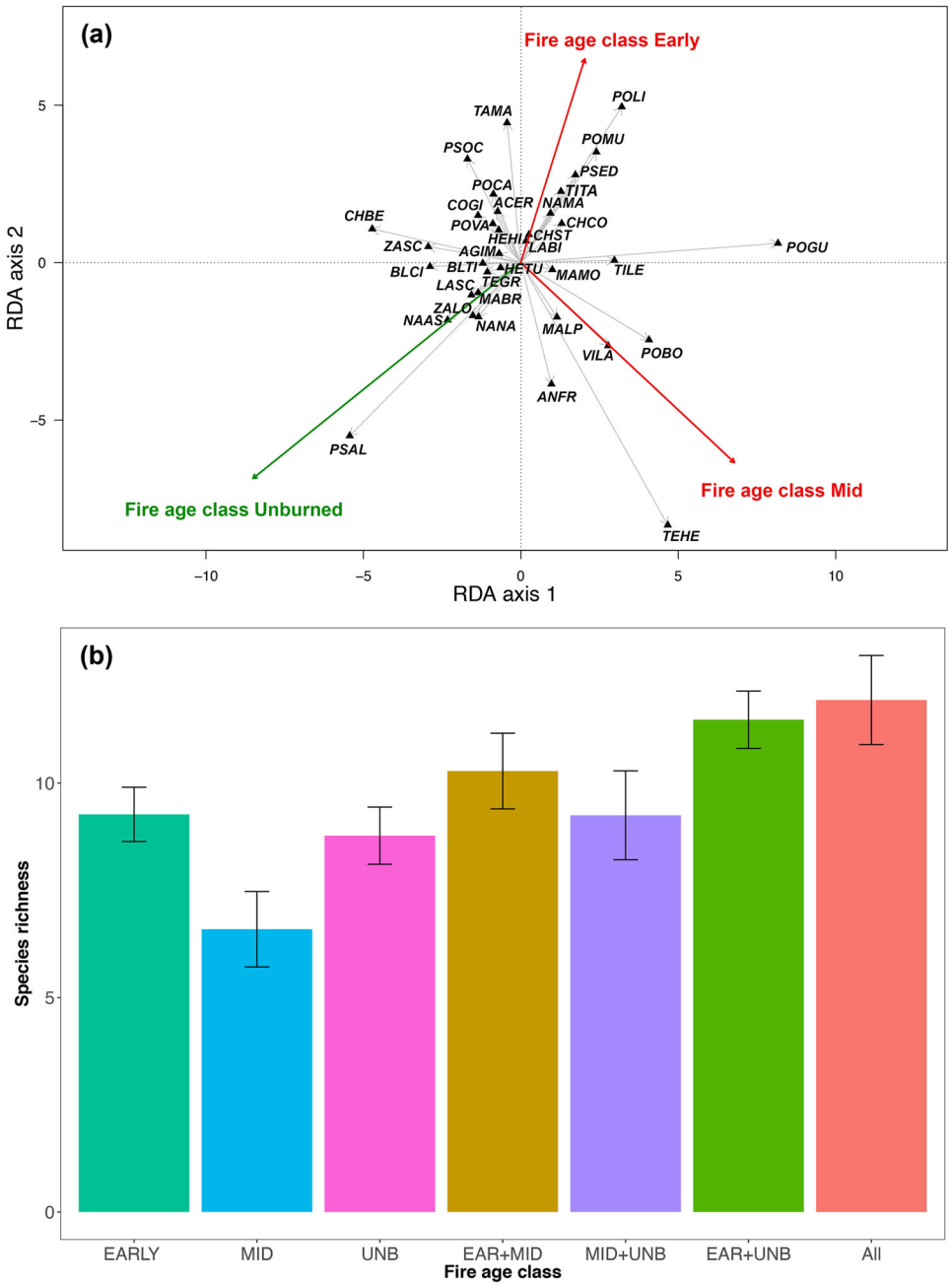

FIGURE 5 (a) Results of redundancy analysis with the reptile species found in trasects and 3 fire age classes (early, middle [MID], and unburned [UNB]) from the western Mediterranean Basin (abbreviations defined in Appendix S5) and (b) mean estimate of the number of species found in each fire age class, in combination of 2 fire age classes, and in combination of the 3 fire age classes (all) per site (whiskers, SE).

confirmed these results (Appendix S9). Species accumulation curves indicated that the number of surveys done at each site were in general enough to characterize the reptile community (Appendix S10).

DISCUSSION

Fire is an integral ecological process. Its complexity has limited the identification of general patterns of animal response at a broad geographic scale. Our results for reptile communities on the western Mediterranean Basin showed that the total number of individuals in recently burned plots was low, and this metric increased in the following years, with a peak at middle fire age plots. Species richness and Shannon diversity showed stable values in early and middle plots. Reptile community metrics maintained higher values under postfire conditions (early and middle) than in unburned (mature) forest plots. Middle plots were underrepresented compared with early and unburned plots; thus, results for total number of

individuals at middle plots have to be interpreted cautiously. However, the pattern observed at early plots, as well as the differences in reptile metrics between early and unburned transects in both afforested and native plots, suggests that Mediterranean reptile communities may exhibit resilience to fire intervals of at least 15 years.

Based on the environmental variables we considered, the range of climatic conditions provided by the study sites allowed us to detect that the 3 reptile metrics varied geographically following rainfall and temperature gradients. Afforestation, a common occurrence in the Mediterranean Basin, had a negative impact on reptile metrics at all fire age classes. The commonest reptile species in the study region, the lizard *P. algirus*, showed some different responses to environmental, habitat, and fire-history variables compared with the community metrics. In the reptile community, saxicolous and mesic species occurred in plots of different fire ages. This result highlights that pyrodiverse landscapes (i.e., a mixture of plots with different fire ages) increased reptile diversity compared with homogeneous landscapes in fire age.

Effect of environmental variables

The study region exhibits spatial climate variability (in the Mediterranean-type climate), with more humidity and colder temperatures toward higher latitudes and altitudes. As expected due to their ectothermic physiology (Huey, 1982) and environmental dependence (Ficetola et al., 2013), reptiles responded to this climate gradient. Communities were more abundant and richer in more humid environments and richer and more diverse in colder environments (in the Mediterranean climate). This trend may be locally mediated by the proliferation of under- and midstory plant species in these environmental conditions. These habitats are structurally complex, attract arthropod prey for reptiles (Pastro et al., 2013), and provide suitable niches (Pinto et al., 2018), factors that enhance reptile communities.

The negative pattern of total number of individuals and Shannon diversity in lower temperature plots may seem counterintuitive for Mediterranean reptiles (see Whiting & Fox, 2021). We speculate that midelevation (colder) plots may host more reptiles than (hotter) lowland plots (as in Fischer & Lindenmayer [2005] and O'Sullivan et al. [2023]) because of a stronger degradation of lowland habitats due to intense human activities, such as agriculture and urbanization (Reidsma et al., 2006; Ribeiro et al., 2009).

Moreover, the climatic trend we observed was partially influenced by the location of the sampled sites (see Figure 1): the northernmost (humid and cold) limit of the sampled region is a transition toward temperate—Atlantic and Continental—ecoregions (Olson et al., 2001). These ecological crossroads show local increases in species richness (Spector, 2002) because each ecoregion has unique reptile assemblages (Smith et al., 2018), and species from different ecoregions can be found in sympatry (Ferreira, Mateus, et al., 2016; Santos & Cheylan, 2013). In fire prone regions, environmental and fire-history gradients are essential for understanding how animal communities are structured at broad geographic scales.

Postfire dynamics

Our results suggest that fire does not negatively affect species richness and Shannon diversity. We found variations in richness (e.g., highest in early and middle plots) and total number of individuals (highest in middle plots) across fire age classes, and both metrics were lowest in unburned sites (Figure 2). Only at short time since the last fire (<6 years) was the total number of individuals low (Figure 4). In the short term, fire leads to abrupt structural changes in the habitat, such as canopy and shrub cover reduction and increases of bare ground (Chergui, Fahd, & Santos, 2018), which in turn can reduce food and shelter availability (Chergui et al., 2019; Hu et al., 2016; Valentine et al., 2012) and suitable microclimates for some reptile species (Webb & Shine, 2008). Thus, a combination of factors, such as direct mortality during fire (Webb & Shine, 2008), changes in habitat structure (Costa et al., 2013), and high predator activity (Senior et al., 2022; Wilgers & Horne, 2007), may result in the short-term pattern we observed.

Despite the low number of individuals found a few years after fire, Mediterranean reptile communities recover when the structure of the forest becomes more complex and thus can hold a rich and abundant reptile community (Pinto et al., 2018). This result supports that Mediterranean reptiles are resilient to fire (Santos et al., 2022), and their responses are linked to successional changes in habitat structure, as has been observed in other fire-prone regions such as Australia (Lindenmayer et al., 2008; Nimmo et al., 2014). Reptile community recovery is faster in natural compared with afforested plots (Muñoz et al., 2021), and species richness seems to not be affected in natural plots. The responses of dominant forest trees to fire can be the underlying cause of differences between both habitat types. Natural forests in the study region are mainly composed of resprouter tree species (*Quercus* species), whereas afforested plots were often dominated by nonresprouting (pine) species that have slower responses to fire. Pines of the study region do not resprout. In addition, afforestation is often linked to reduced resprouting species due to the intense management. In natural forests, the resprouting ability of *Quercus* and other co-occurring species facilitates the resilience of the habitat structure (Chergui, Fahd, & Santos, 2018) that ultimately can buffer the impact of fire on their biotic communities. In contrast, pine sensitivity to fire results in a slow recovery of the habitat complexity reptiles need.

Unburned plots, especially the afforested ones, had the lowest values of the 3 reptile metrics. A dense and homogeneous canopy, as well as the lack of particular structural elements such as sun-exposed rocks, reduces the availability of adequate microhabitats mostly used as refuges for many Mediterranean reptiles (Salvador, 2014), as occurs in other regions of the world (O'Sullivan et al., 2023; Webb et al., 2005).

Reptile community composition varied among fire age classes both in terms of species-specific abundances and occurrence

(see a similar result in Australia; Hu et al., 2013). Differences in abundances can be caused by the short-term impact of fire that is species dependent (Driscoll & Henderson, 2008), whereas differences in occurrence can be related to successional specialization because fire favors certain reptile species and negatively affects others (i.e., early and late successional species, respectively) (Hu et al., 2016; Santos et al., 2016; Smith et al., 2013). Knowledge of specific responses of Mediterranean species to fire is still partial. Some species, such as Mediterranean terrestrial tortoises (genus *Testudo*), experience high mortality due to fire (Couturier et al., 2011), whereas others have evolved mechanisms to deal with fire (Álvarez-Ruiz et al., 2021, 2023). Our study helps identify which species respond to each fire age class. Early-successional reptiles are saxicolous and burrowing species (Santos et al., 2016; Smith et al., 2013), with a preference for open habitats, as is true for many reptile species in Mediterranean climates (Santos & Cheylan, 2013). Species in unburned late successional plots preferred mesic habitats with continuous leaf litter (Costa et al., 2020; Driscoll et al., 2012), as is true for some species thar have a distribution range in the northernmost limit of the Mediterranean climate. The preference of saxicolous and mesic species for early and unburned plots, respectively, suggests that more pyrodiverse landscapes can host richer reptile communities than homogeneous fire age landscapes.

The Algerian psammodromus *P. algirus*, the commonest lizard in the study region, was associated with unburned plots. Modeling the abundance of this lizard demonstrated that it only responded negatively to wildfires in the short term (i.e., early plots) (Figure 3), a result confirmed by 2 before–after wildfire field studies (Moreno-Rueda et al., 2019; Santos et al., 2016). It is a ground-dwelling lizard with a wide ecological valence that lives in many Mediterranean habitats, including edges of pine plantations (Salvador, 2014). Its thermophilic character (it selects higher body temperatures than other sympatric lizards [Ferreira, Santos, et al., 2016]) explains its positive response to temperature and number of fires in the study area. Álvarez-Ruiz et al. (2021) demonstrated that this lizard rapidly detects and reacts to smoke in populations affected by recurrent fire histories, a result that deserves future study to identify whether short-term responses to fire can vary geographically in a single widespread species.

Impact of afforestation

We found that postfire afforested habitats were poorer ecosystems for reptiles than postfire forests that had been less managed. This result supports the general decline observed in reptile communities after anthropogenic habitat changes (Cordier et al., 2021; Doherty et al., 2020). The reptile decline caused by afforestation practices occurred in all fire age classes. Pine afforestation has been an extended practice in the southwestern Mediterranean basin since mid-20th century (Madrigal, 1998; Pausas et al., 2004), and these habitats have lower structural complexity and less diverse flora and fauna than natural forests (Brockerhoff et al., 2008; Chergui, Fahd, & Santos, 2018; da Silva et al., 2019). Afforestation leads to biodiversity loss of many ecosystem components, including arthropods (Prangel et al., 2023), which serve as key prey for many reptile species, particularly lizards. Afforestation practices often reduce sun radiation at the ground level (Mott et al., 2010), ultimately negatively affecting biodiversity (Abreu et al., 2017) and reducing the thermal quality for ectothermic animals (Schreuder & Clusella-Trullas, 2016), such as reptiles (O'Sullivan et al., 2023). Paths and narrow unpaved roads that we used for reptile sampling are the only suitable thermal areas in the afforested matrix for ectotherm organisms (Duchesne et al., 2023). The impact of afforestation practices for reptile fauna (Azor et al., 2015; Gardner et al., 2007) can be especially important for species adapted to open landscapes that need radiation for thermoregulation (i.e., heliotherm species, such as most Mediterranean reptiles) (Salvador, 2014). Although the implications of afforestation practices for biodiversity are debated (Brockerhoff et al., 2008), our results caution against the proliferation of dense tree plantations as a means to enhance biodiversity (Gómez-González et al., 2020).

Future research

The western Mediterranean Basin is experiencing increased frequency and size of fires, as well as length of the fire season (Moreira et al., 2011; Schmuck et al., 2013). The causes of this pattern are well known: increasing warming and drought and an increasing amount and continuity of highly flammable vegetation (Pausas & Fernandez-Muñoz, 2012; Rogers et al., 2020). This fire regime shift could lead to the replacement of forests by scrublands (Moreira et al., 2011). Mediterranean reptile species have exhibited resilience to megafires under favorable environmental conditions (Santos et al., 2022). However, an increased fire recurrence across the Mediterranean region (Pausas, 2022) and the occurrence of megafires can maintain large areas at early successional forest stages, leading to the simplification of the reptile community (Moreira & Russo, 2007). Our study provides evidence that the response of Mediterranean reptiles is species dependent. Ecological specialists and species that live in unburned habitats may be the most sensitive reptile species to this persistent impact. For monitoring this process at a regional scale, our study highlights the importance of considering the interaction between climate variables, habitat type, and fire history to understand reptile patterns in human-transformed areas such as the western Mediterranean Basin.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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