

ARTICLE

Resilience of reptiles to megafires

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Abstract

Extreme climate events, together with anthropogenic land-use changes, have led to the rise of megafires (i.e., fires at the top of the frequency size distribution) in many world regions. Megafires imply that the center of the burnt area is far from the unburnt; therefore, recolonization may be critical for species with low dispersal abilities such as reptiles. We aimed to evaluate the effect of megafires on a reptile community, exploring to what extent reptile responses are spatially shaped by the distance to the unburnt area. We examined the short-term spatiotemporal response of a Mediterranean reptile community after two megafires (>20,000 ha) that occurred in summer 2012 in eastern Spain. Reptiles were sampled over 4 years after the fire in burnt plots located at different distances from the fire perimeter (edge, middle, and center), and in adjacent unburnt plots. Reptile responses were modeled with fire history, as well as climate and remotely sensed environmental variables. In total, we recorded 522 reptiles from 12 species (11 species in the burnt plots and nine in the unburnt plots). Reptile abundance decreased in burnt compared with unburnt plots. The community composition and species richness did not vary either spatially (unburnt and burnt plots) or temporally (during the 4 years). The persistence of reptiles in the burnt area supported their resilience to megafires. The most common lizard species was *Psammotromus algirus*; both adults and juveniles were found in all unburnt and burnt plots. This species showed lower abundances in burnt areas compared with the unburnt and a slow short-term abundance recovery. The lizard *Psammotromus edwardsianus* was much less abundant and showed a tendency to increase its abundance in burnt plots compared with unburnt plots. Within the megafire area, *P. algirus* and *P. edwardsianus* abundances correlated with the thermal–moisture environment and vegetation recovery regardless of the distance from the fire edge. These results indicated the absence of a short-term reptile recolonization from the unburnt zone, demonstrating that reptiles are resilient (*in situ* persistence) to megafires when environmental conditions are favorable.

KEYWORDS

community composition, Mediterranean, megafire, reptiles, satellite remote sensing

INTRODUCTION

Fire is an intrinsic and natural process in many regions, and a key element for understanding the ecology of fire-prone ecosystems (Keeley et al., 2012; Pausas & Keeley, 2009). In those ecosystems, vegetation structure and plant and animal composition are shaped by fire regimes (Kelly et al., 2020; Pausas & Parr, 2018). There is a long standing debate on how fire is affecting biodiversity. First, because species respond to fire in multiple (and sometimes opposed) ways (Ferreira et al., 2016; Moretti et al., 2004); and, second, because there are multiple factors including land-use legacy (Montiel-Molina et al., 2019), vegetation dynamics (Lindenmayer et al., 2008; Swan et al., 2015), fire characteristics (e.g., intensity, size, season, recurrence; Keeley, 2009), and species life-history traits (Smith, 2018) that interact to fully explain the response of organisms to fire. Despite this variability in responses to fire, there is growing evidence that in fire-prone regions plant and animal species are resilient to historical fire regimes (Andersen et al., 2005), and have evolved multiple strategies to respond to this disturbance (Pausas, 2019). In fact, some animals can survive after fire in refugia or protected microsites (Pausas, 2019; Santos et al., 2016); others may temporarily disappear from the burnt area and recolonize from the unburnt area after fire (Brotons et al., 2005). However, the current increase in the frequency of large fires cast doubts on the resilience of animal populations, and especially on those with low mobility and limited dispersal ability.

Given the current anthropogenic effects on fire regime (increased ignitions, land-use changes, and global climate change), the frequency of large fires (e.g., megafires) is increasing worldwide, including the Mediterranean region (Moreira et al., 2020; Pausas & Fernández-Muñoz, 2012). By megafires we refer to those wildfires of high intensity that are at the top of the size frequency distribution of a given region (Pausas & Keeley, 2021). From the biological point of view, a key distinction of megafires is that some burnt areas are very far from the unburnt, and this may limit post-fire colonization. In addition, the increasing drought may imply longer time for vegetation (habitat) to recover (Hislop et al., 2019; Torres et al., 2018) or may move to another stable state (Pausas & Bond, 2020). Therefore, the rise of megafires has increased the level of pressure for biodiversity as animals have to respond to fire at both the temporal (post-fire succession) as well as in the spatial (post-fire recolonization) components (Jones et al., 2016; Jung, 2019; Siegel et al., 2019; Stevens et al., 2012). The spatiotemporal approach is particularly relevant for low-mobility animal species for which megafires are typically much larger than their home range and dispersal distances.

Reptiles are ectotherm organisms (Huey, 1982), and they are sensitive to abrupt shifts in habitat (Doherty et al., 2020) and specifically in vegetation structure (i.e., heterogeneity and cover; Azor et al., 2015). In general, reptiles have small home ranges (Perry and Garland Perry & Garland, 2002, Vitt & Caldwell, 2009) and low dispersal abilities (Valentine & Schwarzkopf, 2008), therefore they can be susceptible to the large high-intensity fires currently occurring in Mediterranean shrublands. Reptiles typically respond to fire with a replacement of species along the post-fire succession process (Hu et al., 2013; Santos & Cheylan, 2013). However, reptiles respond poorly to predictable models of habitat succession as these responses are context dependent (e.g., biogeography, surrounding landscape, climate; Nimmo et al., 2012, 2014; Simms et al., 2019). Therefore, reptile responses largely depend on the rate of vegetation recovery and the resilience of several ecosystem components (Lindenmayer et al., 2008; Santos et al., 2016). Accordingly, megafires can severely compromise reptile recolonization and community composition into the burnt area.

The aim of this study was to evaluate the effect of megafires on a reptile community, exploring how reptile responses are spatially shaped by the distance to external unburnt shrubland, that is, the unburnt vegetation surrounding the burnt area (from this point forward termed “unburnt”). Specifically, we ask whether reptile species survive after a megafire (*in situ* persistence; e.g., hidden in microsites), or alternatively, whether they disappear after fire and colonize from adjacent populations. To answer this question, we sampled reptiles over 4 years after two unusually large fires (>20,000 ha each) in Mediterranean shrublands at eastern Spain. The spatial sampling design included different distances from the unburnt to the center of the fire. Reptile responses were modeled with fire history, as well as climate and remotely sensed environmental variables. These satellite-based variables translated different dimensions of ecosystem functioning linked to energy-matter flows (Alcaraz et al., 2006; Cabello et al., 2012), which recovered with distinct trajectories and speeds after a fire (Marcos et al., 2021; Torres et al., 2018) therefore potentially improving the assessment of reptile responses to megafires. Finding a reptile decline pattern toward the center of the burnt area would suggest that colonization is the main process; the lack of such a pattern may suggest local extinction (if they are absent) or fire survival (if reptiles are present); the latter would support reptile persistence after megafires. The study was conducted over 4 years after the fire disturbance to provide insights into the ecological resilience of the reptile community to megafires.

METHODS

Study sites and sampling design

The study was performed in the Valencia region (eastern Spain), an area with a Mediterranean climate and high fire activity (Pausas, 2004; Pausas & Fernández-Muñoz, 2012). In June/July 2012, two very large fires occurred simultaneously and under extreme weather conditions (very hot and dry weather with strong winds). Fire ignition started in the municipalities of Cortes de Pallás and Andilla (from this point forward, Cortes and Andilla fires) and spread over ~30,000 and 21,000 ha, respectively (Figure 1). According to the fires recorded in the study area during the XIX and XX centuries (see figure 2 in Pausas & Fernández-Muñoz, 2012), fires of this size are in the extreme of the size frequency distribution, and therefore can be considered megafires (see Pausas & Keeley, 2021). The distance between the two fires was ~65 km (straight line), and were located in different mountain chains separated by a valley dedicated to agriculture. Both fires occurred on limestone lithology, and the elevation range of these sites varies from 190 to 1245 m above sea level (asl). Average annual rainfall and temperature for the area are 17.8°C and 454 mm, respectively (www.aemet.es; Spanish Meteorological Agency). Before the 2012 fires, Cortes was a shrubland dominated by *Quercus coccifera*, *Cistus* sp. pl., *Rosmarinus officinalis*, *Juniperus oxycedrus*, and *Brachypodium retusum*, while Andilla alternated similar shrublands with pine

woodlands (*Pinus halepensis*) and some evergreen oak patches (*Quercus ilex*). These differences in vegetation between both sites were mainly attributed to different fire histories previous to the 2012 fires (Pausas et al., 2018). In Cortes, all the area had burnt previously in different fires between 1978 and 1994, and the fire recurrence was higher in the center of the study area than on the edges. In contrast, no fires had been recorded at Andilla in the last 50 years (Figure 1).

In total, 24 plots ~1 ha (12 plots per fire) were sampled over the 4 post-fire years starting the year after the fire (2013–2016), considering different distances in relation to the fire edge (Figure 1): three plots in the surrounding unburnt area (“Unburnt zone”), three plots in the burnt area at less than 500 m from the burnt perimeter (“Edge zone”), three plots in the burnt area at ~1.5 km from the burnt perimeter (“Middle zone”), and three plots in the center of the fire at more than 2 km from the perimeter (“Center zone”). Because of the high intensity of the fires, unburnt patches of natural vegetation inside the burnt area were rare but, in any case, precaution was taken so that plots in the burnt zone were never close to large unburnt patches (e.g., agricultural patches). All sampled plots were located in areas dominated by shrublands, both before the fire for burnt plots and in the unburnt plots, therefore avoiding forest areas. Plot selection also targeted locations where the effect of fire was homogeneous and affected the entire plant structure (i.e., crown-fires). Unburnt plots corresponded to nearby mature shrublands outside the fire perimeter.

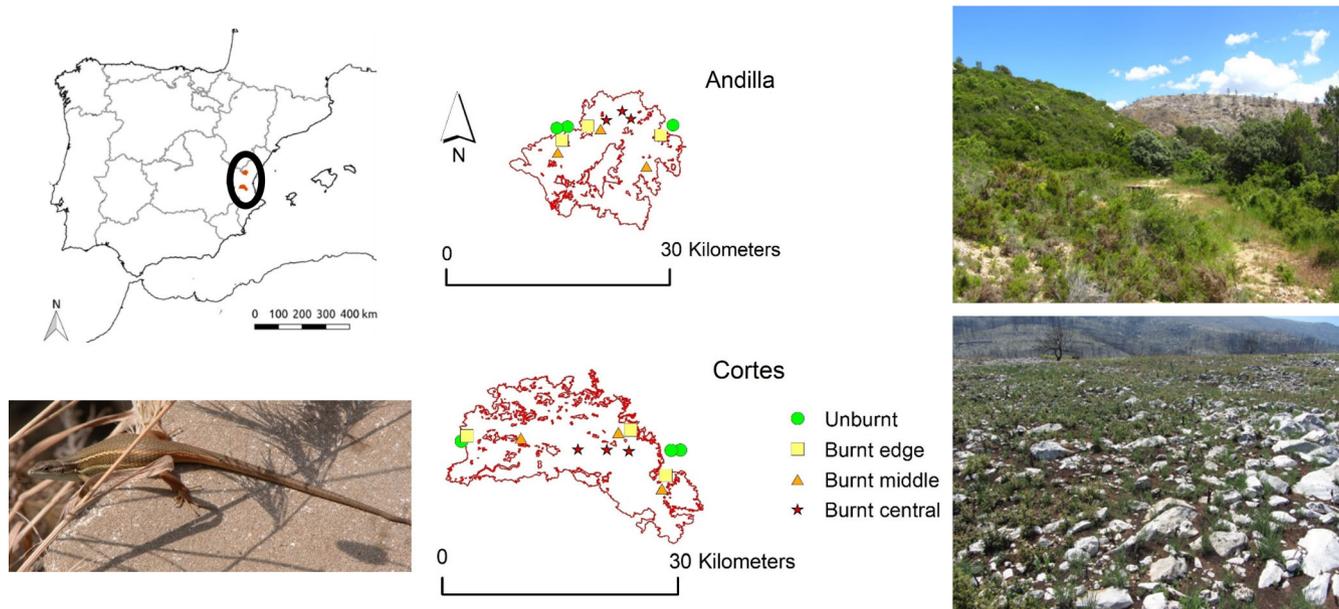


FIGURE 1 Map of the study area in the Iberian context, details of the location of the 24 sampling points and distances to fire perimeter, and photographs of a female *Psammodromus algerius*, and an unburnt and a burnt plot at the area of study

Reptile community variables

At each plot, reptiles were actively searched visually and by turning rocks and other known refuges (as described in Santos & Cheylan, 2013, and Santos et al., 2016) to characterize species composition, abundances, and diversity of the reptile community. Reptile sampling was always conducted in spring (between the April and June months), that is, when reptiles are most active (reproductive period). Each plot was surveyed three times each spring (separated by at least 1 week) by two researchers for periods of 30 min in each visit. Each year, all plots were visited within a 4–5-day period. The search was carried out in sunny days and during reptiles' most active hours. Specimens were identified to species level, sexed, and classified as adult and non-adult individuals when possible. Reptile detectability can vary according to the complexity of the vegetation structure (Chergui et al., 2019). However, previous application of active search sampling in other Mediterranean sites resulted in an unbiased detection of reptile individuals as detection distances were similar in unburnt and burnt plots (Santos et al., 2016; Santos & Cheylan, 2013). For this reason, we did not apply distance correction to our data.

As response variables (reptile community variables) we have used, per plot and year: total reptile abundance and reptile species richness. In all cases the variables were computed after summing the sights in the three surveys made per plot and year. Moreover, as response variables we considered the abundance for the two commonest reptile species, the lizards *Psammmodromus algirus* and *Psammmodromus edwardsianus*.

Environmental variables

Climate data

We used climatic data from the TerraClimate dataset (Abatzoglou et al., 2018), containing monthly climate and climatic water balance for global terrestrial surfaces, and made available by the Google Earth Engine. TerraClimate data are listed at ~4 km of spatial resolution and interpolates high-spatial resolution data from the WorldClim dataset, with coarser spatial resolution, but time-varying data from CRU Ts4.0 and the Japanese 55-year Reanalysis (JRA55; Abatzoglou et al., 2018). Using these data, we calculated annual average anomalies in total annual precipitation (in mm) as well as maximum and minimum temperatures (°C) using a 30-year period of average reference from 1987–2016. Annual anomalies were calculated as the average score of the 12 months before sampling (i.e., from July to June).

Remotely sensed satellite data

We used satellite remote-sensing data (SRSD) to characterize the spatial changes in habitat and vegetation, and capture landscape changes through time (Arenas-Castro et al., 2019; Gonçalves et al., 2016). Specifically, we selected three remote-sensing spectral indices that portray ecological reptile requirements: (1) normalized difference vegetation index (NDVI), which provides a proxy of photosynthetic activity and green biomass (Carlson & Ripley, 1997) and can be used to monitor post-fire dynamics of the reptiles' habitat (e.g., Marcos et al., 2019; Torres et al., 2018); (2) land surface temperature (LST), which provides a surrogate of the thermal environment for reptiles; it is expected to increase after the fire due to changes in albedo (Veraverbeke et al., 2012), and to progressively return to pre-fire conditions with time, making it also suitable for post-fire monitoring; and (3) tasseled caps transform (TCT), a special case of a principal component analysis that transforms the image data to a new coordinate system with a new set of orthogonal axes (Huang et al., 2002; Xiaoyang et al., 2002) that are related to: surface brightness of bare or partially covered soil (and closely linked to albedo, TCTbri), soil or vegetation wetness/water content (TCTwet), and surface greenness linked to vegetation cover (TCTgrn). TCT greenness differs from NDVI by accounting for more spectral information in additional wavelengths from blue to shortwave infrared (~450–2200 nm) and performing a linear combination of all available bands similar to PCA. NDVI formula is more straightforward and based on a normalized ratio that “only” includes reflectance data from the red (~650 nm) and near-infrared (~850 nm) spectral bands. These two indices can be correlated and for this reason a correlation analysis and variance inflation factor were performed to account for TCTgrn–NDVI association.

We obtained NDVI, LST, and TCT data from the following Terra/MODIS satellite platform products: (i) MOD13Q1 product containing 16-day composite images for spectral indices (e.g., NDVI) at 250 m of spatial resolution, (ii) MOD11A1 product containing daily LST data at 1000 m, and (iii) the MOD09A1 product containing Terra/MODIS surface reflectance 8-day composites at 500 m. Image data considered the period 2001–2016 (i.e., 12 years before the fires, and the 4 years of the sampling study).

The image time series obtained for NDVI, LST, and TCT were used to calculate several ecosystem functioning attributes (EFA) that constituted integrative descriptors of ecosystem processes linked to energy and matter flows, as well as seasonal and interannual changes (Alcaraz et al., 2006; Arenas-Castro et al., 2018, 2019; Cabello et al., 2012). EFAs consider the annual distribution of ecosystem process from NDVI, TCT, and LST data to calculate the following

measures: the annual median (Q50) as an index of average quantity and centrality, the interquartile range (Q75%–Q25%; from this point forward IQR) which is a metric of intra-annual seasonal variation, and two extreme values, the 5% and 95% quantiles (Q5 and Q95) that are sensitive to fire severity conditions (Arenas-Castro et al., 2019). For instance, NDVI-IQR is a proxy for seasonal changes in greenness and photosynthetic activity (e.g., deciduous vegetation has relatively higher IQR values than evergreen vegetation). Disturbances such as wildfire can decrease NDVI-IQR after the fire by strongly lowering annual seasonal variation through vegetation burning, lack of photosynthetic activity, and decreasing the NDVI median for the same reasons. All these annual values were calculated considering the 12 months before the sampling (from July to next June of each year).

For all annual EFA variables (i.e., Q50, Q95, Q5, and IQR), we calculated anomalies that allow interannual comparisons between a pre-fire baseline (for period 2001–2011) and the post-fire scenario (2012–2016). The anomaly (a) for a given variable (v), with average for the reference period (\bar{v}), for a certain year (y) is defined as: $a_y = v_y - \bar{v}_{[2001, \dots, 2011]}$. Anomalies can indicate the impact (severity) of the fire on the vegetation structure and the ecosystem functioning as well as the post-fire recovery (“re-greening”) process. For example, immediately after a fire, NDVI-IQR and LST-Q50 anomalies are expected to increase due to very contrasting conditions (vegetated to non-vegetated/burnt) followed by a decrease (depending on vegetation type, fire severity, among other factors). In contrast, the anomaly of the NDVI-Q50 is expected to follow an opposite trend. Drought can also cause strong negative anomalies in NDVI by physiologically limiting growth and decreasing living biomass and hampering the recovery process, while LST will undergo much less changes. Depending on their ability to track meaningful aspects of ecosystem functioning to post-fire reptile survival and recovery, these different EFAs are expected to show widely different predictive ability.

Data analyses

Species accumulation curves using the Chao I and Chao II estimators were performed to assess whether our sampling effort was sufficient for estimating the community composition. Based on the shape of the curve for the total surveys, as well as for burnt and unburnt surveys separately, the asymptotic shape of the Chao I and Chao II estimators against a random accumulation of surveys indicated that our sampling scheme was adequate (Appendix S1: Figure S1). This was confirmed by the occurrence during surveys of all the reptile species historically located on the study region (Pleguezuelos et al., 2002).

Reptile community spatiotemporal variation

Reptile community variables were compared among plots across the four sampling years by permutational multivariate analysis of variance (PERMANOVA). Pairwise similarity in reptile composition among plots was assessed using the Bray–Curtis similarity distance for relative abundance data, and the Jaccard similarity index for presence/absence data. Two PERMANOVA were performed, one to evaluate the effect of fire condition (therefore considering all burnt/unburnt plots), and the other to evaluate the effect of distance to the fire perimeter (therefore only considering burnt plots, edge/middle/center). In both analysis, time since fire (years) and its interaction with fire condition and distance to the fire perimeter were included, and site (Andilla and Cortes) was used as a random factor. This analysis was performed using PRIMER v6 (Clarke & Gorley, 2006).

Environmental predictors' models

Generalized Linear Mixed Models (from this point forward GLMMs) were used to describe the spatiotemporal variation of the environmental predictors at unburnt and burnt plots across the 4 sampling years, and to evaluate how they explained the spatiotemporal variation of the reptile community among plots and years. Similar to the PERMANOVA procedure, we ran two sets of GLMMs: first, including fire condition with the main objective to identify differences between unburnt and burnt plots, and second, only with burnt plots and including the distance to the fire perimeter with the aim to identify differences related to distance.

We considered as predictors (i.e., fixed effects) elevation, four fire-history variables (fire condition [unburnt/burnt], time since the last fire, the number of fires in the last 50 years, and the distance class to the fire perimeter), and 23 environmental variables including climatic data and satellite-derived EFA (see the full list of variables in Appendix S1: Table S1). To make models more parsimonious and avoid spurious effects linked to multicollinearity, we performed pairwise Spearman correlations among environmental variables and removed those with correlation greater than 0.7. With the remaining variables we calculated the variance inflation factors (VIF). VIF value for the best model (see below GLMM procedure) equaled 2.46, and the average for all models in the confidence set ($\Delta AIC_c < 2$) equals 2.85 (min: 1.44; max: 5.18). These values were below the recommended threshold ($VIF \leq 10$; Kutner et al., 2004) indicating very low multicollinearity among predictors.

We used model selection to see which predictor variables better fitted *P. algirus* and *P. edwardsianus*

abundances. The latter was only modeled for the Andilla site as it was almost absent in the Cortes site. In the model development, we specifically considered complex models with multiple predictor variables and their interaction with fire condition. Therefore, we used the “dredge” function (*MuMIn* R package) to build all possible models with a maximum of five combined variables (to reduce potential overfitting issues). This procedure was required to find the best combination of variables and maximize model performance. Models were ranked by their Akaike Information Criterion values (AIC_c ; corrected for small sample sizes). Those models with $\Delta AIC_c < 2$ were considered to have the highest likelihood and support to explain reptile responses. We examined the importance of each variable to explain reptile responses by summing the weights of all models in which each variable had contributed. We also calculated GLMM R^2 values based on Nakagawa and Schielzeth (2013) (*piecewiseSEM* R package) to further assess model fitting and robustness. This statistic splits into conditional- R^2 (including both random and fixed effects) and marginal- R^2 (mR^2 , including solely fixed effects). Reptile abundances (counts of individuals) were modeled assuming a Poisson distribution and using site (Andilla and Cortes) and plot (24 different plots) as random effects.

The *raster* package (Hijmans, 2020) was used to perform all spatial data processing, manipulation and the calculation of satellite-based EFA metrics (among other). Packages *lme4* (Bates et al., 2015), *MuMIn* (Barton, 2020), and *AICcmodavg* (Mazerolle, 2020) were used for data analyses. Packages *ggplot2* (Wickham, 2016) and *sjPlot* (Lüdtke, 2021) were used for producing graphics.

RESULTS

Reptile community composition

We found, in total, 522 reptiles from 12 species (seven lizards and five snakes), 11 species in the burnt plots and nine in the unburnt plots (Table 1). Five species, four lizards (*Tarentola mauritanica*, *Chalcides bedriagai*, *Psammmodromus algirus*, *Psammmodromus edwardsianus*) and one snake (*Malpolon monspessulanum*), were repeatedly found during the 4 years of the study. The most common species was the lizard *P. algirus*, with 79% of the total sights (including adults and juveniles), followed by *P. edwardsianus* with 7.3% of the sights. In burnt plots, we observed juvenile individuals of the four lizard species, supporting reproductive success after the megafires. *P. edwardsianus* has a lifespan of 1 year, and therefore, its persistence in center burnt plots evidences the species resilience to megafires. Three snake species were only

found in burnt plots (*Hemorrhoids hippocrepis*, *Zamenis scalaris*, and *Coronella girondica*). Overall, the number of species per plot ranged from 0 to 4, and abundances of the species per plot ranged from 0 to 5 except for the most common species, *P. algirus*, which reached up to 15 individuals per plot.

Almost the whole reptile community was represented in the burnt plots regardless of the distance to the fire perimeter (Table 2). The commonest species were found even at the center plots more than 2.5 km far from the fire perimeter; moreover, two of the three species exclusively found in burnt areas (*Hemorrhoids hippocrepis* and *Coronella girondica*) were in center plots (Table 2).

There were differences in the reptile community composition (considering species abundances) between burnt and unburnt plots and among years, with a nonsignificant interaction between both factors (Table 3). When considering presence/absence of species, there were no differences between burnt and unburnt plots or among years, and only the site was significant (Table 3).

Among burnt plots, there were differences in the community composition among years and between sites (random factor) but not among the three distance classes (fire edge, middle, and center; Table 3). The results were similar either considering abundance or presence/absence of the species (Table 3).

Spatiotemporal variation of environmental variables

In both unburnt and burnt plots, we observed differences in annual precipitation anomalies across the 4 sampling years, being the second post-fire year very dry (Appendix S1: Figure S2). Interannual differences of the environmental variables were higher and less stable in burnt compared with unburnt plots, with all burnt plots (center, middle and edge) showing the same patterns (Appendix S1: Figure S3). For example, average annual LST anomaly was higher in burnt compared with unburnt plots across all the sampling period (Appendix S1: Figure S3a); the second sampling year (the driest), the average LST anomaly was very high in all the plots (Appendix S1: Figure S3). TCTwet anomaly was significantly higher in burnt compared with unburnt plots for the first 3 sampling years and only was similar among unburnt and burnt plots in the fourth sampling year (Appendix S1: Figure S3b). Annual maximum LST anomaly was stable along the 4 sampling years in unburnt plots, whereas it was extremely high the first year after burning in burnt plots and decreased considerably from the second to the fourth sampling year (Appendix S1: Figure S3c). Annual average NDVI anomaly in unburnt

TABLE 1 Mean number of sight (per plot) of each reptile species observed in unburnt and burnt plots during the 2013–2016 sampling period in Cortes and Andilla megafires (E Iberian Peninsula). The last column includes the percentage of sights of each reptile species (number of sights of one species/total number of sights) as a measure of how dominant each species is in the community. In parentheses is the species code used in Table 2

Species	2013		2014		2015		2016		%
	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt	
<i>Tarentola mauritanica</i> (tm)	0	0.06	0.33	0	1.00	0.50	0	0.39	4.8
<i>Hemidactylus turcicus</i> (ht)	0	0	0.17	0	0.17	0.22	0.17	0	1.3
<i>Chalcides bedriagai</i> (cb)	0	0.17	0	0.17	0.17	0.17	0.17	0.06	2.3
<i>Podarcis liolepis</i> (pl)	1	0.06	0.17	0.06	0	0	0.17	0.17	2.5
<i>Timon lepidus</i> (tl)	0	0	0.17	0.06	0.17	0.06	0	0.06	1
<i>Psammmodromus algirus</i> (pa)	7.33	3.78	4.17	2.11	7.83	2.44	11.33	4.28	79
<i>Psammmodromus edwardsianus</i> (ph)	0	0.28	0.17	0.28	0.17	0.50	1.00	0.61	7.3
<i>Malpolon monspessulanum</i> (mm)	0.17	0.11	0.17	0.06	0	0.06	0.17	0	1.3
<i>Hemorrohis hippocrepis</i> (hh)	0	0.06	0	0	0	0	0	0	0.2
<i>Zamenis scalaris</i> (zs)	0	0	0	0	0	0.06	0	0	0.2
<i>Coronella girondica</i> (cg)	0	0	0	0	0	0	0	0.06	0.2
<i>Vipera latastei</i> (vl)	0	0	0	0	0.17	0	0	0	0.2
Total abundance	8.50	4.50	5.33	2.72	9.67	4.00	13	5.61	
Species richness	0.50	0.39	1.17	0.33	1.17	0.44	1	0.39	

TABLE 2 Reptile species occurrence during the study, specifying those reptiles found only at unburnt, only at burnt, and at both burnt and unburnt plots, during the 4 sampling years, considering the burnt plot distance to the fire perimeter (center, middle, and edge). The aim of this table was not to compare between burnt and unburnt (as the sampling effort was higher in the latter; Figure 1) but to show that, by no means, the diversity of reptiles was concentrated in unburnt plots. *Cases with a higher proportion of juvenile versus adult *P. algirus* in burnt plots. Name of the species as indicated in Table 1

Year	Reptile species occurrence			
	Only at unburnt	Burnt plot distance	Only at burnt	At unburnt and burnt
2013	<i>mm pl</i>	Center	<i>cb ph hh</i>	<i>pa mm</i>
		Middle	–	<i>pa*</i>
		Edge	<i>cb ph tm</i>	<i>pa mm pl</i>
2014	<i>mm ph ht tm tl pl</i>	Center	<i>cb</i>	<i>pa* tl pl</i>
		Middle	<i>cb</i>	<i>pa* mm ph</i>
		Edge	<i>cb</i>	<i>pa ph</i>
2015	<i>ht tl vl cb</i>	Center	–	<i>pa ph cb tm</i>
		Middle	<i>mm</i>	<i>pa* ph ht cb tm tl</i>
		Edge	<i>zs</i>	<i>pa ph ht tm</i>
2016	<i>cb mm ht pl</i>	Center	<i>tl cg</i>	<i>pa* pl ph</i>
		Middle	<i>tm</i>	<i>pa ph</i>
		Edge	<i>tm</i>	<i>pa cb pl ph</i>

plots was stable except for the second year coinciding with the drought, whereas in burnt plots the NDVI anomaly was negative (biomass loss) in the first 2 years after the burning and only increased toward the third year (Appendix S1: Figure S3d).

Reptile responses to environmental predictors

Reptile species richness per plot ranged from 0 to 4 species through all the study period. The best models for

TABLE 3 PERMANOVA results of the reptile community composition of all plots and burnt plots only) in relation to fire condition (unburnt/burnt) site, and distance to fire perimeter (the latter for burnt plots only). In all cases, site was considered a random factor

	Abundance			Presence/absence		
	F	R ²	p	F	R ²	p
All plots						
Fire condition (unburnt/burnt)	8.89	0.19	0.001	1.42	0.05	0.2
Time since fire (1, 2, 3, 4 years)	2.27	0.11	0.01	1.62	0.08	0.07
Fire × time since fire	1.07	0.04	0.4	0.94	0	0.5
Site (Cortes, Andilla)	7.18	0.15	0.001	7.20	0.16	0.001
Burnt plots only						
Burnt distance (edge, middle, center)	1.10	0.03	0.4	1.35	0.06	0.2
Time since fire (1, 2, 3, 4 years)	2.17	0.12	0.03	2.15	0.12	0.01
Burnt plot × time since fire	0.70	0	0.9	0.79	0	0.7
Site (Cortes, Andilla)	6.42	0.18	0.001	6.46	0.18	0.003

richness had weak support due to the low values (explained variances $mR^2 < 0.05$), so they are not shown here. We focused on the most abundant species, the lizards *P. algirus* and *P. edwardsianus*. Both species were present in burnt and unburnt plots and reached abundances up to 15 (*P. algirus*) and five (*P. edwardsianus*) individuals per plot and year. Total reptile abundance models showed very similar results compared with the *P. algirus* abundance models and are not shown here.

The lizard *P. algirus* was more abundant in unburnt than burnt plots across the 4 sampling years (Figure 2). The differences in *P. algirus* abundance between unburnt and burnt plots were important 1 year after the fire, and again 3 and 4 years after the fire. In the second year, however, the abundance in unburnt plots reached the minimum values in accordance with the low annual precipitation (Appendix S1: Figure S2). GLMMs identified 11 models with $\Delta AIC_c < 2$ (R^2_m range ≈ 0.40 – 0.43 ; Appendix S1: Table S2). These models included the three fire variables (i.e., fire condition, the most important variable to explain *P. algirus* abundance, time since fire, and fire recurrence) as well as the interaction of fire condition with time since fire and fire recurrence. The best models also included annual precipitation and three satellite remote-sensing variables (ordered by its importance: aLST-Q50, aTCTwet-Q50, and aLST-Q95; Figure 3a). The interaction aTCTwet-IQR and fire condition were also included among the 11 best models (Appendix S1: Table S3). Overall, *P. algirus* increased at higher annual precipitation (Figure 4a), lower median surface temperatures (aLST-Q50; Figure 4b), and higher soil moisture (aTCTwet-Q50; Figure 4c), and maximum LST (Figure 4d) anomalies.

The lizard *P. algirus* occurred in the three distance classes to unburnt, with newborn individuals found in

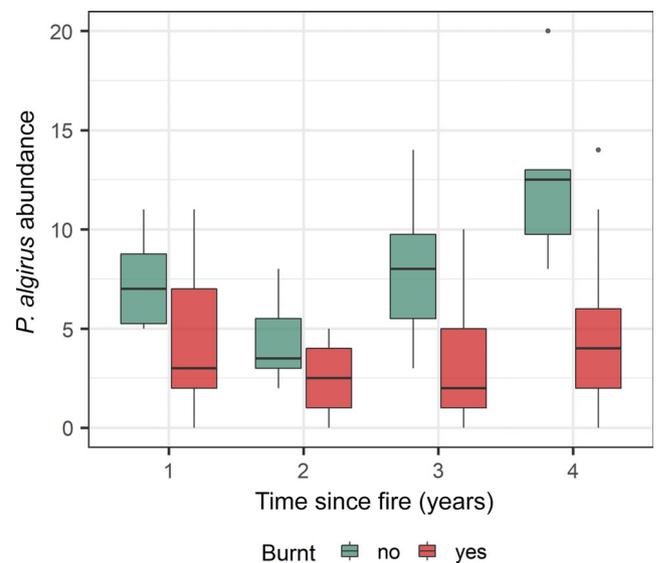


FIGURE 2 Abundance of *Psammodromus algirus* along the 4 sampling years in relation to fire condition (unburnt vs. burnt plots). Boxes indicate the 25%, 50% (median), and 75% quartiles, and lines show minimum and maximum values excluding outliers (indicated as dots)

burnt plots during the 4 years of the field study (Table 2). According to AIC_c -based ranking of models for burnt plots, 19 models were selected with mR^2_c ranging from 0.13 to 0.23, all of them including two variables, that is, median LST (aLST-Q50) and fire recurrence (Appendix S1: Table S4). When we order all the variables according to their importance in the model selection, fire recurrence and several environmental variables were more important to explain *P. algirus* abundance than time since fire and distance to the fire perimeter (Figure 3b). GLMM results showed that, among burnt plots, its

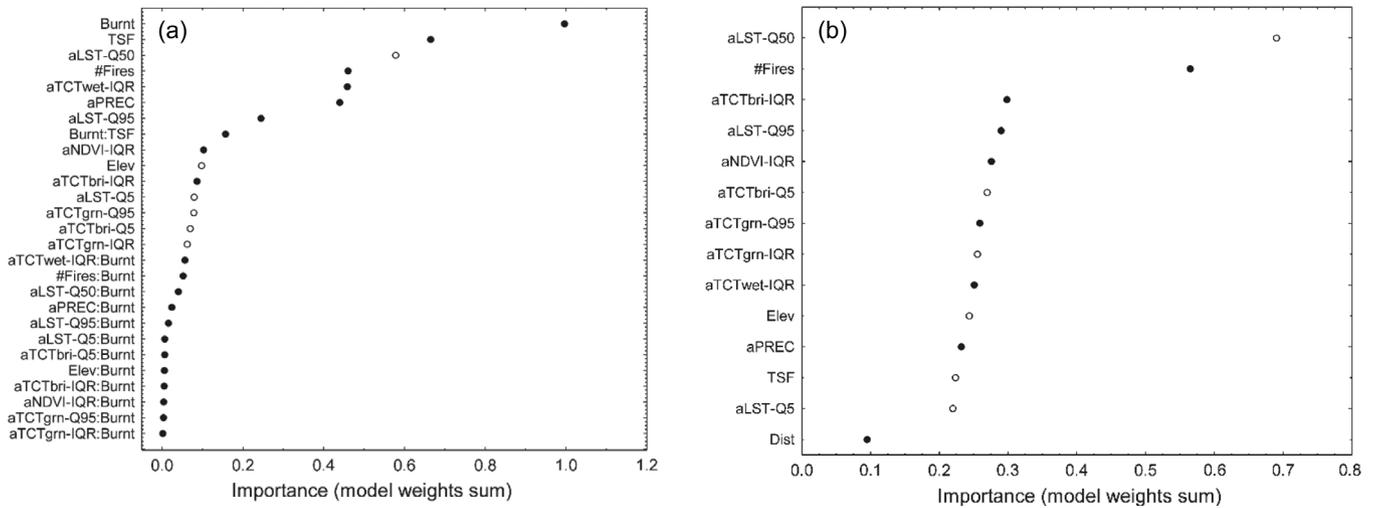


FIGURE 3 Ranking of the importance of explanatory variables considered to model *Psammodromus algirus* abundance. Analyses included: (a) unburnt and burnt plots, and the variable fire condition (burnt); and (b) only burnt plots, and the variable distance to fire perimeter (Dist). Filled dots refer to positive effects and open dots to negative effects based on coefficient estimates. Variable names are: *Burnt*: fire condition (yes/no), *Dist*: plot distance to fire perimeter (edge, middle, center), *Elev*: elevation, *#Fires*: number of fires, *TSF*: time since fire in years; remotely sensed variables names: *aLST*: land surface temperature anomaly, *aTCT*: tasseled caps transform anomaly (for *wetness*, *greenness* and *brightness* components), *aNDVI*: normalized difference vegetation index anomaly. The suffix for these latter variables relates to the annual statistic calculated: *Q50* (median), *Q5* (5% percentile), *Q95* (95% percentile), and *IQR* (interquartile range)

abundance increased for LSTs closer to pre-fire conditions (i.e., values of LST anomaly closer to zero) and higher levels of vegetation greenness (aTCTgrn-Q95), as well as in plots with high fire recurrence, whereas the distance to the fire perimeter was not significant.

The lizard *P. edwardsianus* only occurred in Andilla, and was observed in two unburnt plots out of three, and in seven burnt plots out of nine (Table 2). According to the AIC_c scores, the best models showed that *P. edwardsianus* abundance increased at burnt plots compared with unburnt plots, and at higher altitudes. Moreover, *P. edwardsianus* was more abundant in plots of higher aTCTwet-IQR and aTCTbri_Q05, and lower aLST_Q50 (Appendix S1: Table S5, Figure S4).

DISCUSSION

Our field study, combined with fire-history, climatic, and satellite remote-sensing variables, suggested that: (1) megafires reduced the abundance of reptiles but did not affect the overall community composition; (2) there was evidence of fire survival in lizards (adults and eggs) after megafire; (3) there was a lack of spatial (i.e., no pattern from edge to center) post-fire lizard responses in the burnt area; (4) *P. algirus* did not evidence abundance recovery in the 4 post-fire years; and (5) in the burnt area, spatial and temporal variability in environmental anomalies (i.e., the amount of change in relation to pre-fire

conditions) and past fire history better explained *P. algirus* abundance than spatial attributes. These results suggested that post-fire survival is a more prominent fire strategy (“refugia and dormant” see Pausas, 2019) than exogenous colonization, and therefore reptiles showed persistence to large fires. Holling’s (1973) seminal paper defined resilience as a measure of the persistence of systems and of their ability to absorb changes after disturbance. Despite the reduction of *P. algirus* abundance, the occurrence of all reptile species in burnt plots suggested some resilience capacity of the reptile community. This resilience is caused by their persistence after the fire and not by their colonization ability from unburnt areas.

Compared with other vertebrate groups with higher mobility, reptiles have very small home ranges. In an extensive study with 222 lizard data sets, Perry and Garland (2002) observed that most lizard species have home ranges below 0.02 km². Only lizards of the family Varanidae had larger home ranges in accordance with their large body size, as home range and body size are correlated in reptiles (Perry & Garland, 2002) and mammals (Kelt & Van Vuren, 2001). Despite the larger dispersion abilities of many mammals compared with reptiles, *in situ* survival and not recolonization from the unburnt was also the mechanism of post-fire recovery of mammal populations in Australian megafires (Banks et al., 2011; Hale et al., 2021). The key factor that explains wildlife resistance to fire is the presence of refuges in the burnt area (Hale et al., 2021; Robinson et al., 2013). Habitat

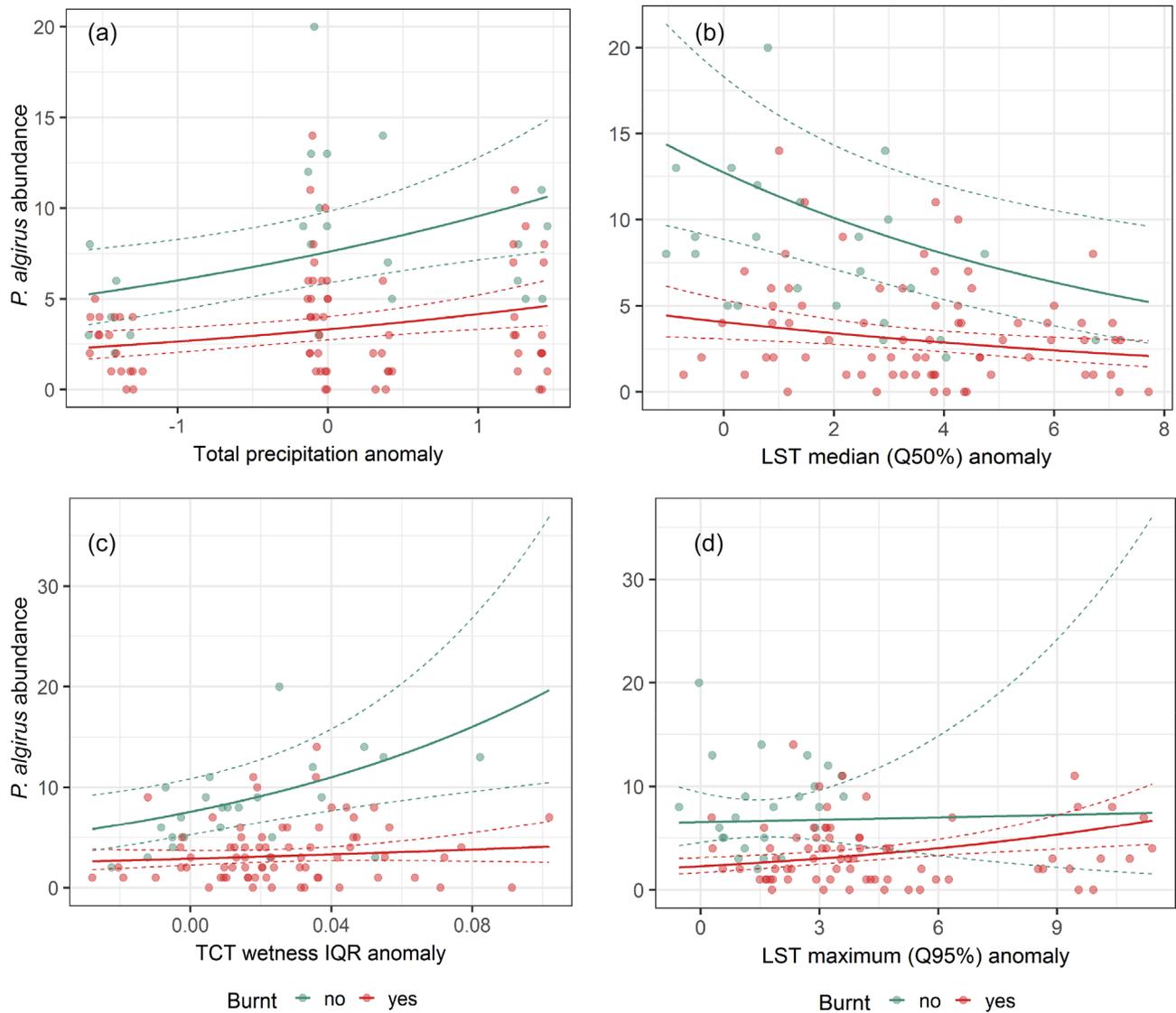


FIGURE 4 *P. algrus* abundance in relation to environmental variables for unburnt and burnt plots. Lines are the predicted values (GLMM models) with their confidence interval: (a) annual precipitation, (b) median annual LST, (c) median annual TCT wetness, and (d) maximum annual LST anomalies

structures in the burnt area enhance fauna survival during the fire event, facilitating population persistence, and community resilience; for this reason, those reptile species that use structures not consumed by the flames (e.g., rocks and big boulders) are more resilient to fire than those associated with vegetation (Ferreira et al., 2019; Santos et al., 2016). The maintenance and post-fire restoration of these structures can guide stakeholders to reduce the impact of megafires on wildlife.

Community composition

During field surveys we found all 12 species known to occur in the study region (Pleguezuelos et al., 2002). Although the two studied sites (Andilla and Cortes)

slightly differed in their reptile communities, the mega-fire only reduced the abundance of reptiles within each site but did not affect the community composition (e.g., no local extinction of any reptile species). Post-fire changes of the reptile community composition after a forest fire are a general result worldwide (Abom & Schwarzkopf, 2016; Ferreira, Mateus, & Santos, 2016; Santos et al., 2016) and can be caused by direct individual mortality (Jordaan et al., 2020; Smith et al., 2012) and by a drastic modification of the habitat (Costa et al., 2020). These two factors in concert can favor the abundance of species with preference for open habitats, in the short term (Hu et al., 2016), that would be substituted by species of forested habitats from long-unburnt patches (Santos & Cheylan, 2013). However, we did not detect local extinction nor positive responses (increased

abundance) of any reptile species caused by the high-intensity megafires. In fact, for patches with higher fire recurrence within the megafire perimeters (e.g., three times in 50 years; central Cortes fire), reptile richness and *P. algirus* abundance showed higher scores than in areas burnt only once. This suggests that Mediterranean reptile species found in both sites are well suited to those fire-prone shrublands in limestone landscapes. The long history of fires in the study region (Pausas & Fernández-Muñoz, 2012) might have regulated the composition of the reptile community as occurs in other ecosystem components (McLauchlan et al., 2020).

***Psammodromus* lizards spatiotemporal dynamic**

The presence of juveniles of *P. algirus* and the presence of *P. edwardsianus* (a small lizard with a 1-year lifespan) in the first year since the fires confirmed that individuals and their eggs could survive hidden underground, and therefore the persistence of these species are ensured. *Psammodromus* is a genus of small lizards from the Mediterranean basin characterized by their long tail and overlapping dorsal scales that allowed them to reduce water loss. These lizard species inhabited Mediterranean shrublands, and *P. algirus* can be considered a generalist reptile from an ecological point of view as it inhabits all type of Mediterranean vegetation such as scrublands, grasslands, oak, and pine forest understory both in pristine and also degraded landscapes (Salvador, 2015). In these habitats, *Psammodromus* lizards escape from predators by quickly moving to vegetation roots where they can survive the flames. In fact, *P. algirus* can recognize the threat of fire by detecting the smoke (Álvarez-Ruiz et al., 2021), which triggers a behavioral response to hide in those fire-protected microsites.

Although *P. algirus* is considered a fast colonizer of disturbed habitats (Márquez-Ferrando et al., 2009) and it can even benefit from post-fire environments (e.g., lower parasitic load; Álvarez-Ruiz et al., 2021), in this study it showed no evidence of neither post-fire colonization from unburnt (no spatial pattern) nor *in situ* recovery of the abundance during the 4 years after the megafires (Figure 2). This slow recovery could suggest that some plots had suboptimal environmental conditions for reptiles after the megafires. For example, dry and harsh conditions, as well as limestone outcrops, may have limited plant regrowth in many burnt plots during the 4 post-fire sampling years. Additionally, the study area experienced a severe drought 2 years after the fire that affected both unburnt and burnt plots. Fast vegetation regrowth (e.g., herbaceous plants) is a major factor in the understanding of short-term reptile recovery

(Lindenmayer et al., 2008). Herbaceous plants can soon attract insect pollinators and other arthropods (Pausas et al., 2018) that are a food source for most Mediterranean lizard species such as *P. algirus* (Salvador, 2015). Moreover, vegetation regrowth can improve microenvironmental conditions such as moisture at the ground level. Experimentally, *P. algirus* was demonstrated to select body temperatures between 34–36°C and to suffer limited water stress in a dry environment compared with other Iberian lizards (Ferreira et al., 2016; Sannolo & Carretero, 2019). Despite its physiological characteristics and wide ecological valence (Salvador, 2015), burnt plots showed notable differences in *P. algirus* abundance (from a complete absence of reptiles to abundances similar to unburnt plots) that were more related to environmental variations than to distance from unburnt areas.

Concluding remarks

The use of remote-sensing data has allowed monitoring of the spatiotemporal environmental variation that was correlated with *P. algirus* and *P. edwardsianus* abundance. These techniques provided complementary insights into in-field quantification of vegetation and structural layers (Chergui et al., 2019; Nimmo et al., 2014; Pastro et al., 2013) to better understand and predict the response of ectotherm species to megafires.

The irruption of extreme climate events coupled with fuel accumulation in human occupied systems are promoting megafires. Reptiles survived the megafires (adults and eggs) and they were present into the burnt area during the 4 sampling years. Despite the limited recovery of the commonest lizard species, the reptile community showed a resilience capacity for large fires. The lack of any spatial pattern (distance to unburnt) suggests that post-fire survival and local population persistence from refugia is a more prominent fire strategy than exogenous colonization for vagile species such as reptiles.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Santos et al., 2021) are available from the Figshare repository: <https://doi.org/10.6084/m9.figshare.16553607>

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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