

## 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 centre of the burned area is far from the unburnt; thus, 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 unburned area. We examined the short-term spatiotemporal response of a Mediterranean reptile community after two megafires (>20.000 hectares) occurred in summer 2012 at eastern Spain. Reptiles were sampled during four years after the fire in burnt plots located at different distances from the fire perimeter (edge, middle, and centre), and in adjacent unburnt plots. Reptile responses were modelled 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 9 in the unburnt plots). Reptile abundance decreased in burnt compared to unburnt plots. The community composition and species richness did not vary either spatially (unburnt and burnt plots) or temporally (along the four years). The persistence of reptiles in the burnt area supports 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 to the unburnt and a slow short-term abundance recovery. The lizard *P. edwardsianus* was much less abundant and showed a tendency to increase its abundance at burnt plots compared to 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 indicate 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 favourable.

**Key words:** 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 (Pausas and Keeley 2009, Keeley et al. 2012). In those ecosystems, vegetation structure and plant and animal composition are shaped by fire regime (Kelly et al. 2020, Pausas and 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 (Moretti et al. 2004, Ferreira et al. 2016b); and, secondly, 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 (Santos et al. 2016, Pausas 2019); others may temporarily disappear from the burnt area and recolonize from the unburnt area after fire (Brotons et al. 2005). However, the current raise 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 (Pausas and Fernandez-Muñoz 2012, Moreira et al. 2020). By megafires we refer to those wildfires of high intensity that are in the top of the size frequency distribution of a given region (Pausas and 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 postfire colonization. In addition, the increasing drought may imply longer time for vegetation (habitat) to recover (Torres et al. 2018, Hislop et al. 2019) or may move to another stable state (Pausas and Bond 2020). Thus, the rise of megafires has increased the level of pressure for biodiversity since animals have to respond to fire at both the temporal (post-fire succession) as well as in the spatial (post-fire recolonization) components (Stevens et al. 2012, Jones et al. 2016, Jung 2019, Siegel et al. 2019). 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 2002, Vitt and Caldwell 2009) and low dispersal abilities (Valentine and Schwarzkopf 2008), thus 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 and 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., 2014, 2012; Simms et al., 2019). Thus, 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, *i.e.*, the unburnt vegetation surrounding the burnt area (hereafter 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 during four years after two unusually large fires (>20,000 ha each) in Mediterranean shrublands at eastern Spain. The spatial sampling design includes different distances from the unburnt to the centre of the fire. Reptile responses were modelled with fire history, as well as climate and remotely sensed environmental variables. These satellite-based variables translate different dimensions of ecosystem functioning linked to energy-matter flows (Alcaraz et al. 2006, Cabello et al. 2012), which recover with distinct trajectories and speeds after a fire (Torres et al. 2018, Marcos et al. 2021) thus potentially improving the assessment of reptile responses to megafires. Finding a reptile decline pattern towards the centre of the burnt area would suggest that colonization is the main process; the lack of such 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 along four years after the fire disturbance to provide insights on the ecological resilience of the reptile community to megafires.

## Material and 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 and Fernandez-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 (hereafter, Cortes and Andilla fires) and spread over ca. 30,000 and 21,000 ha, respectively (Fig. 1). According to the fires recorded in the study area during the XIX and XX centuries (see Fig. 2 in Pausas & Fernandez-Muñoz 2012), fires of this size are in the extreme of the size frequency distribution, and thus can be considered megafires (*sensus* Pausas & Keeley 2021). The distance between the two fires was ca. 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 a.s.l. Average annual rainfall and temperature for the area are 17.8°C and 454 mm, respectively ([www.aemet.es](http://www.aemet.es); Spanish Meteorological Agency). Before the 2012 fires, Cortes was a shrubland dominated by *Q. 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 centre of the study area than on the edges. In contrast, no fires were recorded at Andilla in the last 50 years (Fig. 1).

A total of 24 plots ca. 1 ha (12 plots per fire) were sampled during four post-fire years starting the year after the fire (2013-2016), considering different distances in relation to the fire edge (Fig. 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 *ca.* 1.5 km from the burnt perimeter ('Middle zone'), and three plots in the centre of the fire at more than 2 km from the perimeter ('Centre 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 in the case of burnt plots, and in the unburnt plots, thus 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.

### ***Reptile community variables***

At each plot, reptiles were actively searched visually and by turning rocks and other known refuges (as described in Santos and 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 April-June months), i.e., when reptiles are most active (reproductive period). Each plot was surveyed three times each spring (separated by at least one week) by two researchers for periods of 30 minutes 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 and Cheylan 2013, Santos et al. 2016). 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 *Psammodromus algirus* and *Psammodromus 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 is at ~4Km 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 which portray ecological reptile requirements: 1) Normalized Difference Vegetation Index (NDVI),

which provides a proxy of photosynthetic activity and green biomass (Carlson and Ripley 1997) and can be used to monitor post-fire dynamics of the reptiles' habitat (e.g., Torres et al. 2018, Marcos et al. 2019); 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 components analysis which 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 which '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 land surface temperature data at 1000m, and (iii) the MOD09A1 product containing Terra/MODIS surface reflectance 8-day composites at 500m. Image data considered the period 2001-2016 (i.e., twelve years before the fires, and the four years of the sampling study).

The image time series obtained for NDVI, LST, and TCT were used to calculate several Ecosystem Functioning Attributes (EFA) which constitute integrative descriptors of ecosystem processes linked to energy and matter flows, as well as seasonal and inter-annual changes (Alcaraz et al. 2006, Cabello et al. 2012, Arenas-Castro et al. 2018, 2019). 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 inter-quartile range (Q75% - Q25%; hereafter IQR) which is a metric of intra-annual seasonal variation, and two extreme values, the 5% and 95% quantiles (Q5 and Q95) which 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 inter-annual comparisons between a pre-fire baseline (for period 2001-2011) and the post-fire scenario (2012 – 2016). The anomaly ( $a_y$ ) 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 EFA's are expected to show widely different predictive ability.

### ***Data analyses***

Species accumulation curves using the Chao I and Chao II estimators were performed in order 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 indicate that our sampling scheme was adequate (Appendix S1: Fig. S1). This is 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 with 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 (thus considering all burnt/unburnt plots), and the other to evaluate the effect of distance to the fire perimeter (thus only considering burnt plots, edge/middle/centre). 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 with PRIMER v6 (Clarke and Gorley 2006).

### ***Environmental predictors' models***

Generalized Linear Mixed Models (hereafter GLMMs) were used to describe the spatiotemporal variation of the environmental predictors at unburnt and burnt plots across the four sampling years, and to evaluate how they explain the spatiotemporal variation of the reptile community among plots and years. Similar to PERMANOVA procedure, we run 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 ecosystem functioning attributes (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) equals 2.46, and the average for all models in the confidence set ( $\Delta\text{AICc} < 2$ ) equals 2.85 (min: 1.44, max: 5.18). These values are 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 fit *P. algirus* and *P. edwardsianus* abundances. The latter was only modelled in Andilla site as it was almost absent in Cortes site. In the model development, we specifically considered complex models with multiple predictor variables and their interaction with fire condition. Thus, 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 (AICc; corrected for small sample sizes). Those models with  $\Delta AICc < 2$  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 has 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 a total of 522 reptiles from 12 species (seven lizards and five snakes), 11 species in the burnt plots and 9 in the unburnt plots (Table 1). Five species, four lizards (*Tarentola mauritanica*, *Chalcides bedriagai*, *Psammotromus algirus*, *Psammotromus edwardsianus*) and one snake (*Malpolon monspessulanum*), were repeatedly found during the four 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 one year, and thus, its persistence in centre 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 centre 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 centre plots (Table 2).

There were differences in the reptile community composition (considering species abundances) between burnt and unburnt plots and among years, with a non significant 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 centre; 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 four sampling years, being the second post-fire year very dry (Appendix S1: Fig. S2). Inter-annual differences of the environmental variables were higher and less stable in burnt compared to unburnt plots, with all burnt plots (centre, middle and edge) showing the same patterns (Appendix S1: Fig. S3). For example, average annual LST anomaly was higher in burnt compared to unburnt plots across all the sampling period (Appendix S1: Fig. S3a); the second sampling year (the driest), the average LST anomaly was very high in all the plots (Appendix S1: Fig. S3). TCTwet anomaly was significantly higher in burnt compared to unburnt plots the first three sampling years and only were similar among unburnt and burnt plots the fourth sampling year (Appendix S1: Fig. S3b). Annual maximum LST anomaly was stable along the four 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: Fig. S3c). Annual average NDVI anomaly in unburnt plots was stable except for the second year coinciding with the drought, whereas in burnt plots NDVI anomaly was negative (biomass loss) in the first two years after the burning and only increased towards the third year (Appendix S1: Fig. 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 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 5 (*P. edwardsianus*) individuals per plot and year. Total reptile abundance models showed very similar results than *P. algirus* abundance models and are not shown here.

The lizard *P. algirus* was more abundant in unburnt than burnt plots across the four sampling years (Fig. 2). The differences in *P. algirus* abundance between unburnt and burnt plots were important one year after the fire, and again 3 and 4 years after the fire. The second year however, the abundance in unburnt plots reached the minimum values in accordance to the low annual precipitation (Appendix S1: Fig. S2). GLMMs identified 11 models with  $\Delta AICc < 2$  ( $R^2m$  range  $\approx 0.40-0.43$ ; 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; Fig. 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 (Fig. 4a), lower median surface temperatures (aLST-Q50; Fig. 4b), and higher soil moisture (aTCTwet-Q50, Fig. 4c), and maximum LST (Fig. 4d) anomalies.



The lizard *P. algirus* occurred in the three distance classes to unburnt, with newborn individuals found in burnt plots during the four years of the field study (Table 2). According to AICc-based ranking of models for burnt plots, 19 models were selected with  $mR^2c$  ranging from 0.13 to 0.23, all of them including two variables, i.e. median land surface temperature (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 (Fig. 3b). GLMM results showed that, among burnt plots, its abundance increased for land surface temperatures closer to pre-fire conditions (i.e. values of land surface temperature 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 AICc scores, the best models showed that *P. edwardsianus* abundance increased at burnt plots compared to 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 and Fig. S4).

## Discussion

Our field study, combined with fire-history, climatic, and satellite remote sensing variables, suggest 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 centre) post-fire lizard responses in the burnt area; 4) *P. algirus* did not evidence abundance recovery in the four 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 suggest that post-fire survival is a more prominent fire strategy ('refugia and dormant' *sensu* Pausas 2019) than exogenous colonization, and thus reptiles show 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 suggests certain 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 to 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 km<sup>2</sup>. Only lizards of the Family Varanidae had larger home ranges in accordance to their large body size, as home range and body size are correlated in reptiles (Perry and Garland, 2002) and mammals (Kelt and Van Vuren, 2001). Despite the larger dispersion abilities of many mammals compared to reptiles, *in situ* survival and not recolonization from the unburnt was also the mechanism of postfire 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 (Robinson et al., 2013; Hale et al., 2021). Habitat structures in the burnt area enhance fauna survival during the fire event, facilitating population persistence, and community resilience; for this reason, those reptile species which use structures not consumed by the flames (e.g., rocks and big boulders) are more resilient to fire than those associated to

vegetation (Santos et al., 2016; Ferreira et al., 2019). The maintenance and postfire restoration of these structures can guide stakeholders to reduce the impact of megafires on wildlife.

### ***Community composition***

During field surveys we found all twelve 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 megafire 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 (Santos et al. 2016, Abom and Schwarzkopf 2016, Ferreira et al. 2016b) and can be caused by direct individual mortality (Smith et al. 2012, Jordaan et al. 2020) and by a drastic modification of the habitat (Costa et al. 2020). These two factors in concert can favour the abundance of species with preference for open habitats, at the short term, (Hu et al. 2016) that would be substituted by species of forested habitats from long-unburnt patches (Santos and 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 and 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 of one-year lifespan) in the first year since fire confirms that individuals and their eggs can survive hidden underground, and thus 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 allow them to reduce water loss. These lizard species inhabit 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 like 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 it can survive to the flames. In fact, *P. algirus* can recognize the threat of fire by detecting the smoke (Álvarez-Riuz et al. 2021a), which triggers a behavioral response to hide in those fire-protected microsites.

Despite *P. algirus* is considered a fast colonizer of disturbed habitats (Márquez-Ferrando et al. 2009) and it can even benefit from postfire environments (e.g. lower parasitic load; Álvarez-Ruiz et al. 2021b), in this study it showed no evidence of neither post-fire colonization from unburned (no spatial pattern) nor in-situ recovery of the abundance during the four years after megafires (Fig. 2). This slow recovery could suggest that some plots had suboptimal environmental conditions for reptiles after the megafire. For example, dry and harsh conditions, as well as limestone outcrops, may limit plant re-growth in many burnt plots during the four post-fire sampling years. Additionally, the study area experimented a severe drought two years after the fire which affected both unburnt and burnt plots. Fast vegetation re-growth (e.g. herbaceous plants) is a major factor to understand short-term reptile recovery (Lindenmayer et al. 2008). Herbaceous plants can soon attract insect pollinators and other

arthropods (Pausas et al. 2018) that are food source for most Mediterranean lizard species such as *P. algirus* (Salvador 2015). Moreover, vegetation regrowth can improve micro-environmental conditions such as moisture at the ground level. Experimentally, *P. algirus* has demonstrated to select body temperatures between 34-36° C and to suffer limited water stress in a dry environment compared to other Iberian lizards (Ferreira et al. 2016a, Sannolo and 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 the spatiotemporal environmental variation that resulted to be correlated with *P. algirus* and *P. edwardsianus* abundances. These techniques provide complementary insights to in-field quantification of vegetation and structural layers (Pastro et al. 2013, Nimmo et al. 2014, Chergui et al. 2019) 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 megafires (adults and eggs), and they were present into the burnt area during the four sampling years. Despite the limited recovery of the commonest lizard species, the reptile community shows resilience capacity to 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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**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 brackets are the species code used in Table 2.

Species	Year		2013		2014		2015		2016		%
	Fire condition		no	yes	no	yes	no	yes	no	yes	
<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>Psammodromus algirus</i> (pa)			7.33	3.78	4.17	2.11	7.83	2.44	11.33	4.28	79
<i>Psammodromus 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>Hemorrhois 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	

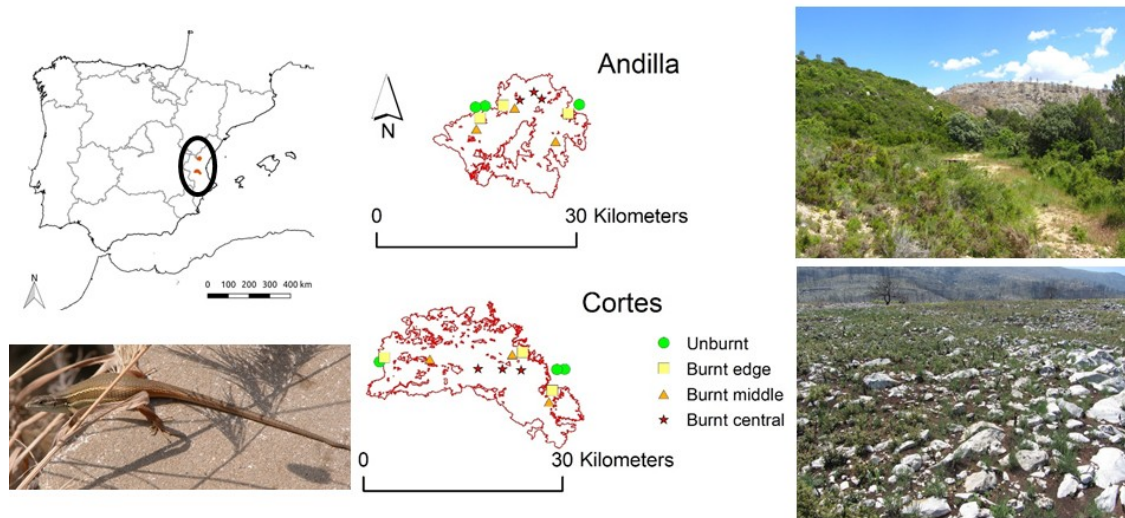
**Table 2.** Reptile species occurrence along the study, specifying those found only at unburnt, only at burnt, and at both burnt and unburnt plots, during the four sampling years, considering the burnt plot distance to the fire perimeter (centre, middle, and edge). The aim of this table is not to compare between burnt and unburnt (as the sampling effort was higher in the latter; Fig. 1) but to show that by no means the diversity of reptiles is concentrated in unburnt plots. \*: cases with higher proportion of juvenile vs adult *P. algirus* in burn plots. Name of the species as indicated in Table 1.

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

**Table 3.** PERMANOVA results of the reptile community composition 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 as a random factor.

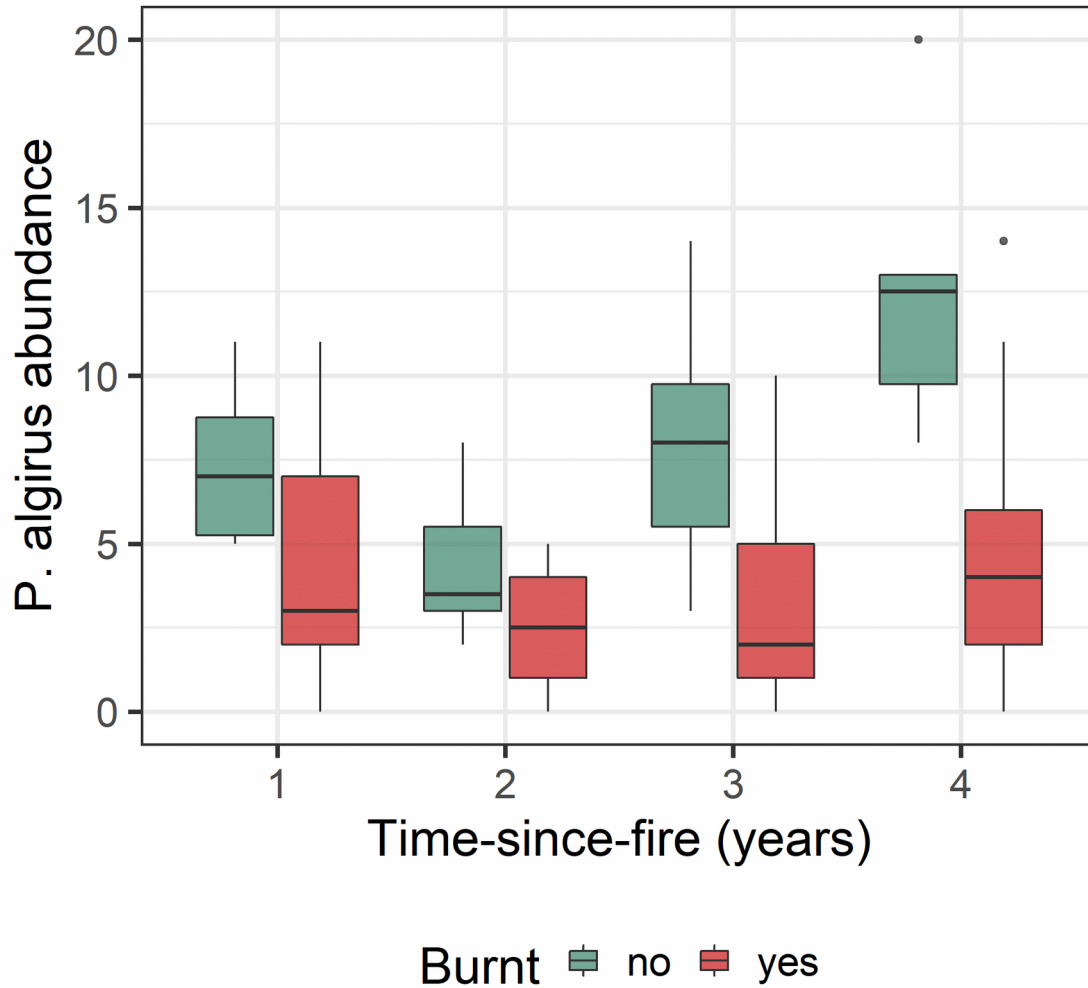
	Abundance			Presence/absence		
	F	R <sup>2</sup>	P	F	R <sup>2</sup>	P
<b>All plots</b>						
Fire condition (unburnt/burnt)	8.89	0.19	<b>0.001</b>	1.42	0.05	0.2
Time since fire (1, 2, 3, 4 years)	2.27	0.11	<b>0.01</b>	1.62	0.08	0.07
Fire * Time since fire	1.07	0.04	0.4	0.94	0	0.5
Site (Cortes, Andilla)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

Figure 1



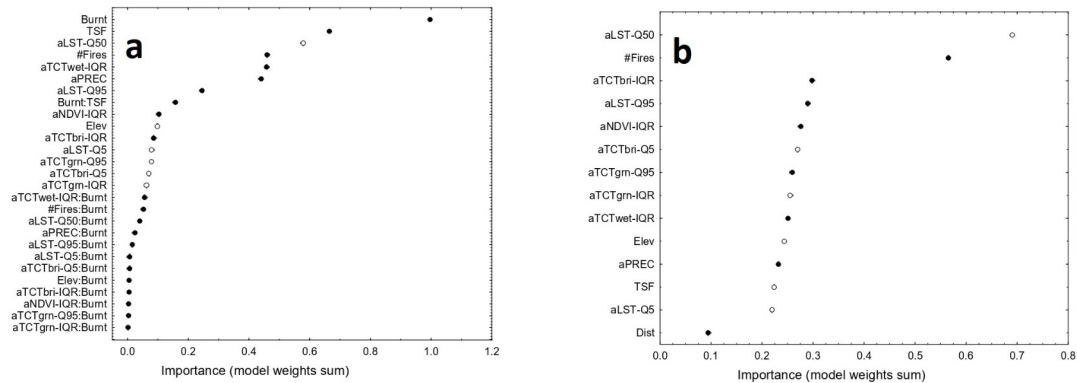
**Figure 1:** Map of the study area in the Iberian context, detail of the location of the 24 sampling points and distances to fire perimeter, and pictures of a female of *Psammodromus algirus*, an unburnt and a burnt plot at the area of study.

Figure 2



**Figure 2:** Abundance of *Psammodromus algerius* along the four 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).

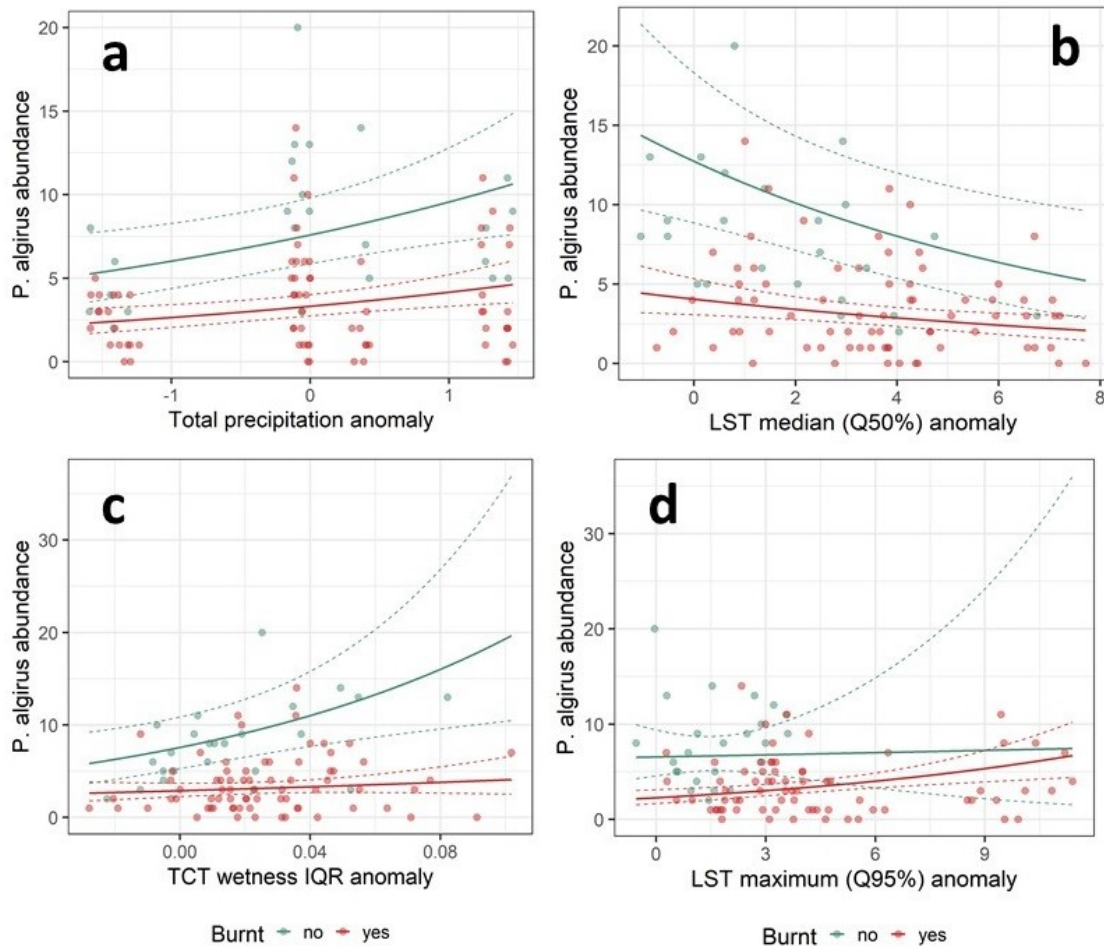
Figure 3



**Figure 3:** Ranking of the importance of explanatory variables considered to model *Psammmodromus 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, centre), *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* (inter-quartile range).



Figure 4



**Figure 4:** *P. algirus* 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.

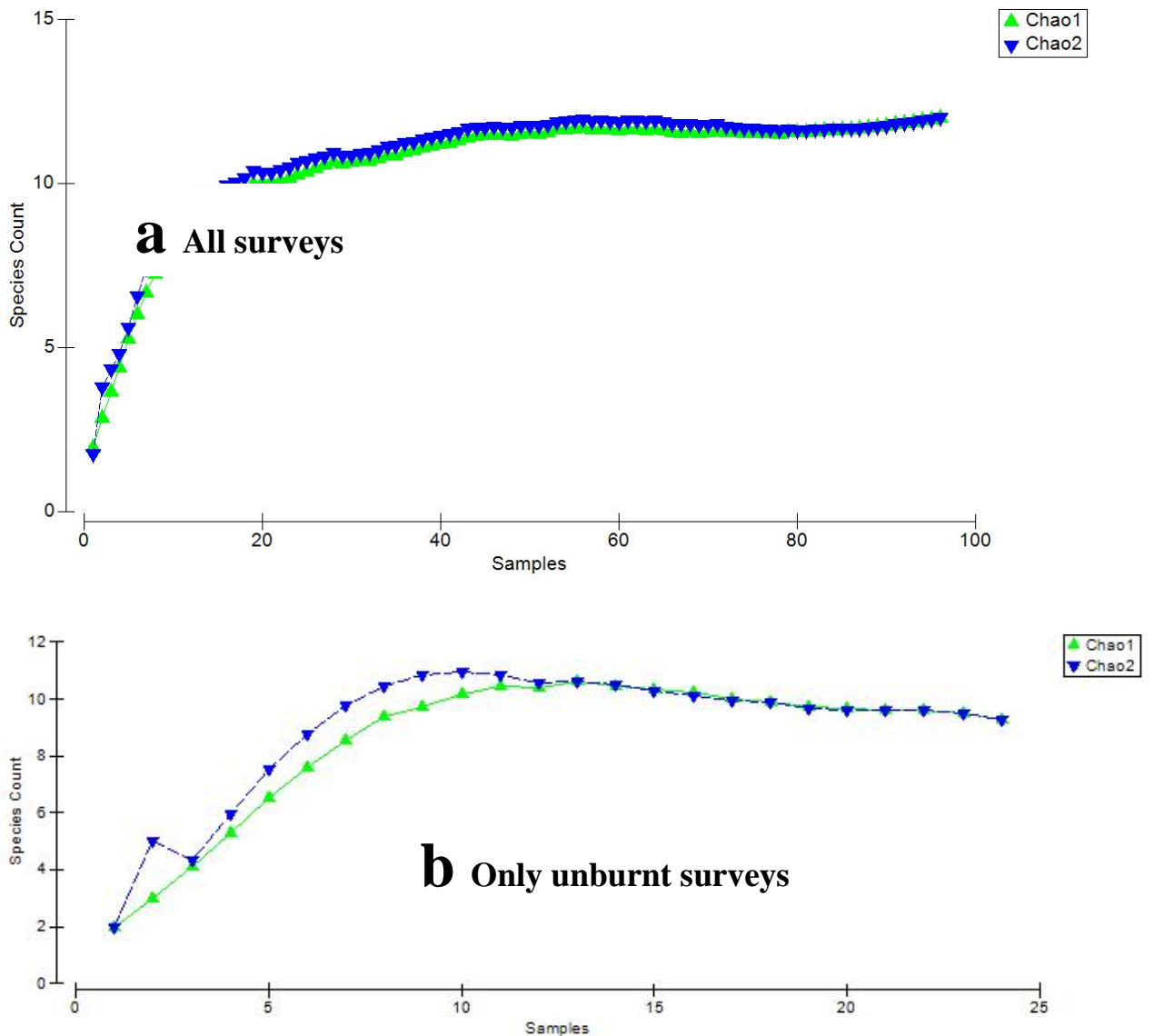
## Supplementary Material

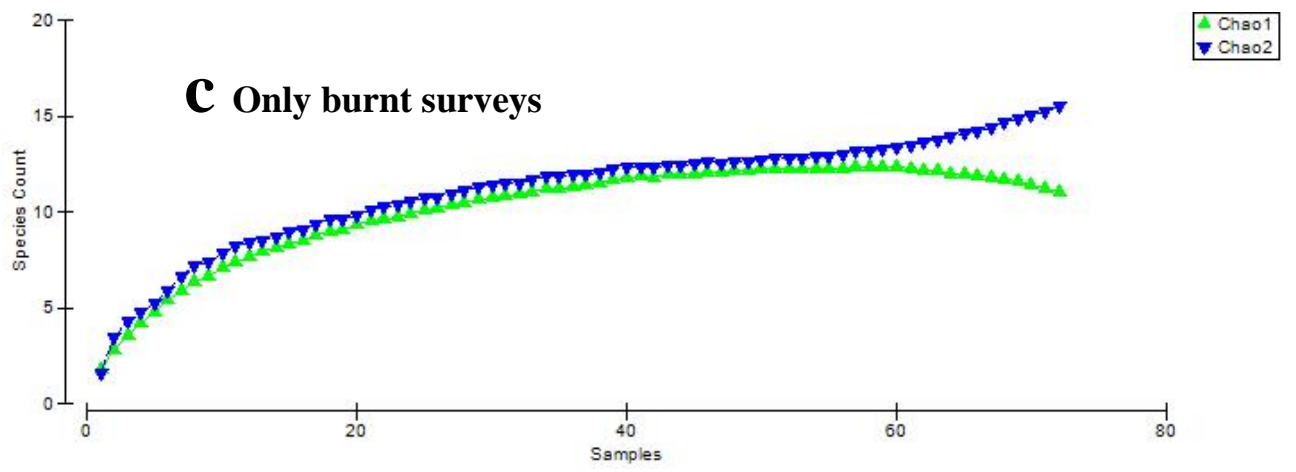
**Authors:** Xavier Santos, Josabel Belliure, Joao Gonçalves, Juli G. Pausas

**Title:** Resilience of reptiles to megafires

**Journal:** Ecological Applications

**Figure S1:** Species accumulation curves showing an estimate of species richness (species counts) based on a matrix of abundance data (Chao I) and presence-absence data (Chao II). These estimators are calculated from a randomly increased number of samples from the total number of surveys (a), only unburnt surveys (b) and only burnt surveys (c).

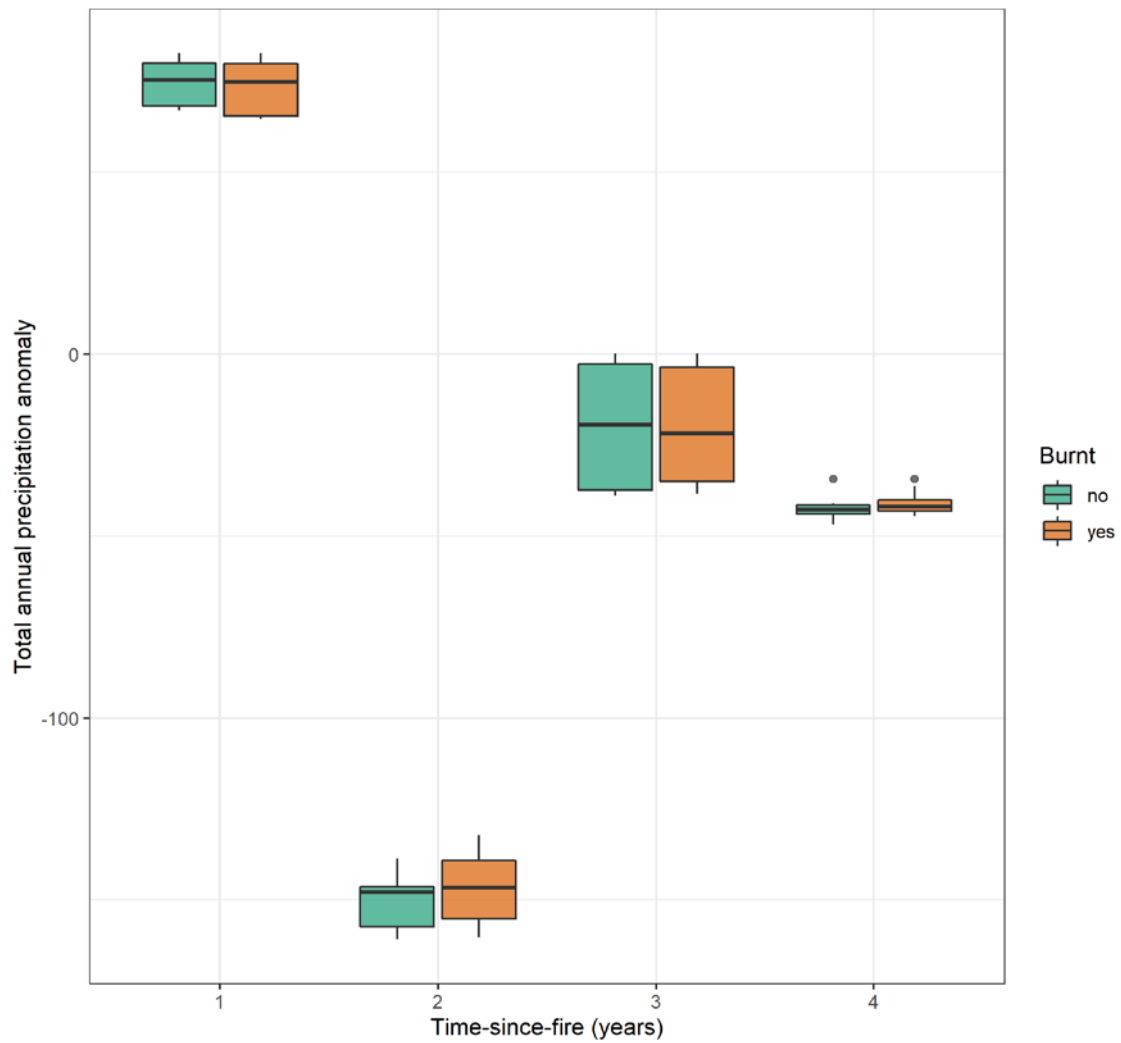




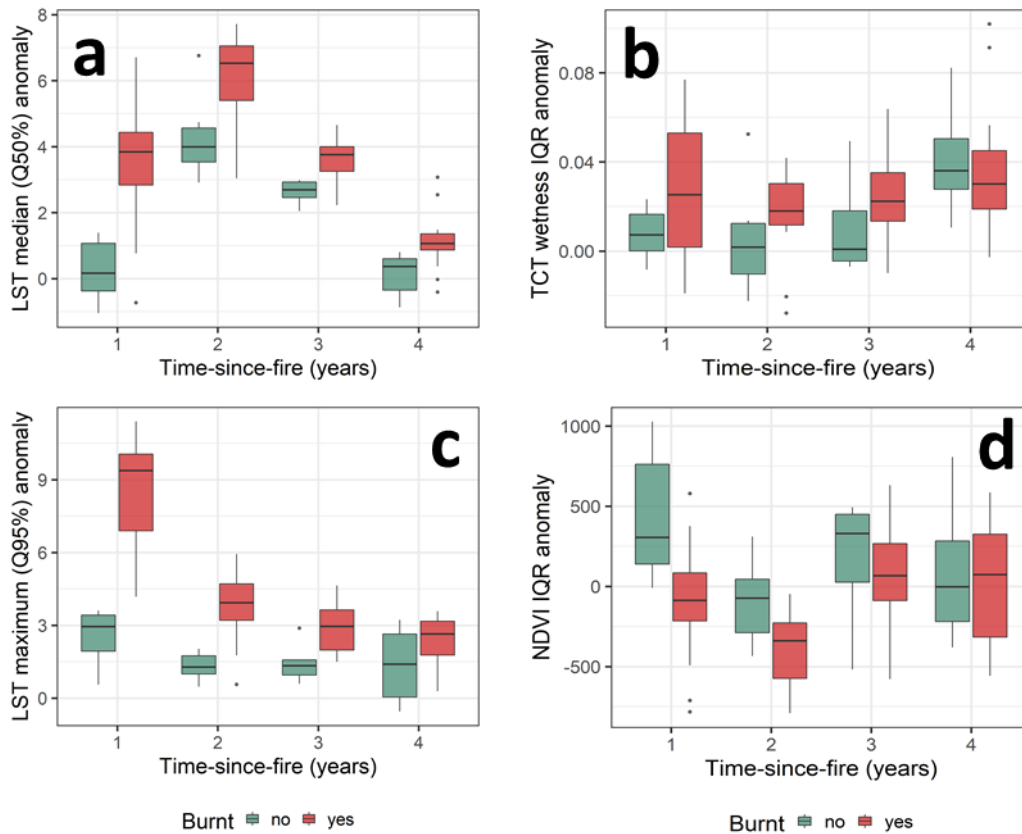
**Table S1:** Description of the 28 predictive variables (fixed factors) assessed to characterize each sampling plot and to be used in model development. Variables included Elevation, four fire history variables, and 23 environmental variables. (a) refers that the anomaly of the variable was used in the statistical analyses. Anomalies were calculated by comparing the average annual score of twelve months (July to June) before the field sampling with a pre-fire reference period (2001-2012). NDVI: Normalized Difference Vegetation Index; LST: Land Surface Temperature; TCT: Tasselled caps transform; TCTbri: brightness; TCTwet: wetness; TCTgrn: greenness. The last column shows variables included in the modelling analysis after excluding correlated predictors (see more details in the text). \*Fire condition and Distance to the fire perimeter were included in the GLMM analysis with all the sampling plots and only with burnt plots, respectively.

<b>Variables</b>	<b>Description</b>	<b>Variables included</b>
<b>Elev</b>	Elevation (in meters a.s.l.)	Yes
<b>Burnt</b>	Fire condition (unburnt and burnt)	Yes*
<b>TSF</b>	Time-since-fire (1, 2, 3, and 4 years since 2012)	Yes
<b>#Fires</b>	Number of fires in the last 50 years	Yes
<b>Dist</b>	Distance to the fire perimeter (edge, medium and centre)	Yes*
<b>aPrec</b>	Total annual precipitation (mm)	Yes
<b>aMinT</b>	Annual minimum temperature (°C)	No
<b>aMaxT</b>	Annual maximum temperature (°C)	No
<b>aNDVI-Q50</b>	Annual average NDVI	No
<b>aNDVI-Q95</b>	Annual 0.95 quantile NDVI	No
<b>aNDVI-Q5</b>	Annual 0.5 quantile NDVI	No
<b>aNDVI-IQR</b>	Annual inter-quartile range (25%-75%) NDVI	Yes
<b>aLST-Q50</b>	Annual average LST	Yes
<b>aLST-Q95</b>	Annual 0.95 quantile LST	Yes
<b>aLST-Q5</b>	Annual 0.5 quantile LST	Yes
<b>aLST-IQR</b>	Annual inter-quartile range (25%-75%) LST	No
<b>aTCTbri-Q50</b>	Annual average TCTbri	No
<b>aTCTbri-Q95</b>	Annual 0.95 quantile TCTbri	No
<b>aTCTbri-Q5</b>	Annual 0.5 quantile TCTbri	Yes
<b>aTCTbri-IQR</b>	Annual inter-quartile range (25%-75%) TCTbri	Yes
<b>aTCTwet-Q50</b>	Annual average TCTwet	No
<b>aTCTwet-Q95</b>	Annual 0.95 quantile TCTwet	No
<b>aTCTwet-Q5</b>	Annual 0.5 quantile TCTwet	No
<b>aTCTwet-IQR</b>	Annual inter-quartile range (25%-75%) TCTwet	Yes
<b>aTCTgrn-Q50</b>	Annual average TCTgrn	No
<b>aTCTgrn-Q95</b>	Annual 0.95 quantile TCTgrn	Yes
<b>aTCTgrn-Q5</b>	Annual 0.5 quantile TCTgrn	No
<b>aTCTgrn-IQR</b>	Annual inter-quartile range (25%-75%) TCTgrn	Yes

**Figure S2:** Variation of the annual precipitation in unburnt and burnt plots during the four years after the fire. Boxes indicate the 25, 50% (median) and 75% quartiles, and lines show minimum and maximum values without outliers.



**Figure S3:** Variation of the remote-sensing environmental variables in unburnt and burnt plots (for the best GLMM model) along the four sampling years after the fire: (a) Median Annual Land Surface Temperature (LST); (b) Median annual tasselled aps transform (TCT) wetness; (c) Maximum Annual Land Surface Temperature (LST); and (d) Median Annual Normalized Difference Vegetation Index (NDVI). Boxes indicate the 25%, 50% (median) and 75% quartiles, and lines show minimum and maximum values without outliers.



**Table S2.** Model ranking of the variables that better explain *Psammodromus algirus* abundance in two megafires at Valencia province (E Iberian Peninsula). Lizard sampling was conducted in unburnt and burnt plots during four years after the fire. The ranking was based on AICc values and only models with  $\Delta$  AICc < 2 are considered. Each row represents a model, and includes a description of the parameters and the variables used. Codes are the same as in Table S1. VIF: (Maximum) Variance Inflation Factor.

Model	df	AICc	Delta_AICc	AICc weight	mR <sup>2</sup>	VIF	Model description
1	8	491,961	0	0,150	0,431	2.46	Burnt, TSF, #Fires, aLST-Q50, aLST-Q95
2	8	492,137	0,175	0,137	0,406	4.85	Burnt, TSF, #Fires, aLST-Q50, Burnt*TSF
3	8	492,244	0,283	0,130	0,434	2.25	Burnt, TSF, #Fires, aPREC, aTCTwet-IQR
4	8	492,575	0,614	0,110	0,420	5.18	Burnt, TSF, #Fires, aPREC, Burnt*TSF
5	7	493,291	1,330	0,078	0,416	2.22	Burnt, #Fires, aLST-Q50, aTCTwet-IQR
6	7	493,291	1,330	0,078	0,416	2.41	Burnt, #Fires, aLST-Q50, aTCTwet-IQR, Burnt*#Fires
7	8	493,514	1,553	0,069	0,437	2.69	Burnt, TSF, #Fires, aPREC, aLST-Q95
8	7	493,537	1,576	0,069	0,435	2.27	Burnt, TSF, #Fires, aPREC
9	7	493,537	1,576	0,069	0,435	2.74	Burnt, TSF, #Fires, aPREC, Burnt*#Fires
10	8	493,821	1,860	0,059	0,406	2.82	Burnt, #Fires, aLST-Q50, aTCTwet-IQR, Burnt* aTCTwet-IQR
11	7	493,923	1,962	0,056	0,391	1.44	Burnt, TSF, aPREC, aTCTwet-IQR



**Table S3.** Results of the best models for *P. algirus* abundance in Valencia megafires based on model averaging procedure and data dredging.

**Best model 1: Marginal R<sup>2</sup> = 0.515**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	10.18 ***	0.16	2.32	7.50 – 13.81	2.01 – 2.63	14.89
aLST_Q50	0.82 **	0.06	-0.20	0.72 – 0.92	-0.32 – -0.08	-3.27
aLST_Q95	1.26 **	0.08	0.23	1.08 – 1.47	0.08 – 0.39	2.92
Burnt [yes]	0.29 ***	0.21	-1.22	0.20 – 0.44	-1.63 – -0.82	-5.93
#Fires	1.23 *	0.09	0.21	1.03 – 1.47	0.03 – 0.39	2.29
TSF	1.22 **	0.07	0.20	1.08 – 1.39	0.07 – 0.33	3.09

• *p*<0.05 \*\* *p*<0.01 \*\*\* *p*<0.001

**Best model 2: Marginal R<sup>2</sup> = 0.447**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	8.78 ***	0.17	2.17	6.34 – 12.14	1.85 – 2.50	13.11
aLST_Q50	0.77 ***	0.06	-0.26	0.68 – 0.87	-0.39 – -0.13	-4.05
Burnt [yes]	0.36 ***	0.21	-1.02	0.24 – 0.55	-1.44 – -0.60	-4.76
#Fires	1.31 **	0.10	0.27	1.08 – 1.58	0.08 – 0.46	2.81
TSF	1.24 **	0.07	0.22	1.08 – 1.42	0.08 – 0.35	3.11
Burnt [yes] * TSF	0.77 **	0.09	-0.27	0.64 – 0.92	-0.45 – -0.08	-2.84

• *p*<0.05 \*\* *p*<0.01 \*\*\* *p*<0.001

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**Best model 3: Marginal R<sup>2</sup> = 0.527**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	9.92 ***	0.16	2.29	7.25 – 13.58	1.98 – 2.61	14.32
aPREC_SUM	1.23 ***	0.06	0.21	1.09 – 1.38	0.09 – 0.32	3.48
aTCTwet_IQR	1.12	0.06	0.11	1.00 – 1.26	-0.00 – 0.23	1.89
Burnt [yes]	0.30 ***	0.21	-1.19	0.20 – 0.46	-1.61 – -0.78	-5.68
#Fires	1.23 *	0.09	0.20	1.02 – 1.47	0.02 – 0.39	2.15
TSF	1.21 ***	0.05	0.19	1.09 – 1.35	0.09 – 0.30	3.55

• *p*<0.05    \*\* *p*<0.01    \*\*\* *p*<0.001

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**Best model 4: Marginal R<sup>2</sup> = 0.465**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	9.72 ***	0.15	2.27	7.22 – 13.08	1.98 – 2.57	14.99
aPREC_SUM	1.26 ***	0.06	0.23	1.12 – 1.41	0.11 – 0.34	3.89
Burnt [yes]	0.31 ***	0.20	-1.16	0.21 – 0.47	-1.55 – -0.76	-5.78
#Fires	1.25 *	0.09	0.22	1.05 – 1.49	0.05 – 0.40	2.49
TSF	1.39 ***	0.07	0.33	1.21 – 1.61	0.19 – 0.47	4.51
Burnt [yes] * TSF	0.84	0.09	-0.17	0.70 – 1.01	-0.35 – 0.01	-1.83

• *p*<0.05    \*\* *p*<0.01    \*\*\* *p*<0.001

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**Best model 5: Marginal R<sup>2</sup> = 0.521**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	9.20 ***	0.18	2.22	6.49 – 13.04	1.87 – 2.57	12.45
aLST_Q50	0.81 ***	0.06	-0.22	0.72 – 0.90	-0.33 – -0.10	-3.80
aTCTwet_IQR	1.16 **	0.06	0.15	1.04 – 1.30	0.04 – 0.27	2.64
Burnt [yes]	0.33 ***	0.23	-1.09	0.21 – 0.53	-1.55 – -0.64	-4.75
#Fires	1.26 *	0.10	0.23	1.03 – 1.55	0.03 – 0.44	2.26

• *p*<0.05    \*\* *p*<0.01    \*\*\* *p*<0.001

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**Best model 6: Marginal R<sup>2</sup> = 0.521**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	9.20 ***	0.18	2.22	6.49 – 13.04	1.87 – 2.57	12.45
aLST_Q50	0.81 ***	0.06	-0.22	0.72 – 0.90	-0.33 – -0.10	-3.80
aTCTwet_IQR	1.16 **	0.06	0.15	1.04 – 1.30	0.04 – 0.27	2.64
Burnt [yes]	0.33 ***	0.23	-1.09	0.21 – 0.53	-1.55 – -0.64	-4.75
#Fires	1.26 *	0.10	0.23	1.03 – 1.55	0.03 – 0.44	2.26

• *p*<0.05 \*\* *p*<0.01 \*\*\* *p*<0.001

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**Best model 7: Marginal R<sup>2</sup> = 0.483**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	10.51 ***	0.15	2.35	7.81 – 14.13	2.06 – 2.65	15.55
aLST_Q95	1.15	0.09	0.14	0.97 – 1.36	-0.03 – 0.31	1.57
aPREC_SUM	1.21 **	0.06	0.19	1.07 – 1.37	0.07 – 0.32	2.98
Burnt [yes]	0.28 ***	0.20	-1.26	0.19 – 0.42	-1.66 – -0.87	-6.28
#Fires	1.21 *	0.09	0.19	1.02 – 1.45	0.02 – 0.37	2.16
TSF	1.34 ***	0.06	0.29	1.18 – 1.51	0.17 – 0.41	4.68

• *p*<0.05 \*\* *p*<0.01 \*\*\* *p*<0.001

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**Best model 8: Marginal R<sup>2</sup> = 0.480**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	9.92 ***	0.15	2.29	7.39 – 13.33	2.00 – 2.59	15.23
aPREC_SUM	1.26 ***	0.06	0.23	1.12 – 1.41	0.11 – 0.34	3.92
Burnt [yes]	0.30 ***	0.20	-1.19	0.21 – 0.45	-1.58 – -0.80	-5.96
#Fires	1.25 *	0.09	0.22	1.05 – 1.49	0.05 – 0.40	2.49
TSF	1.26 ***	0.05	0.23	1.14 – 1.39	0.14 – 0.33	4.66

• *p*<0.05 \*\* *p*<0.01 \*\*\* *p*<0.001

**Best model 9: Marginal R<sup>2</sup> = 0.480**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	9.92 ***	0.15	2.29	7.39 – 13.33	2.00 – 2.59	15.23
aPREC_SUM	1.26 ***	0.06	0.23	1.12 – 1.41	0.11 – 0.34	3.92
Burnt [yes]	0.30 ***	0.20	-1.19	0.21 – 0.45	-1.58 – -0.80	-5.96
#Fires	1.25 *	0.09	0.22	1.05 – 1.49	0.05 – 0.40	2.49
TSF	1.26 ***	0.05	0.23	1.14 – 1.39	0.14 – 0.33	4.66
Burnt * #Fires	(dropped term)	-	-	-	-	-

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

**Best model 10: Marginal R<sup>2</sup> = 0.445**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	9.43 ***	0.17	2.24	6.73 – 13.22	1.91 – 2.58	13.04
aLST_Q50	0.81 ***	0.06	-0.21	0.72 – 0.90	-0.32 – -0.10	-3.73
aTCTwet_IQR	1.26 **	0.08	0.23	1.07 – 1.48	0.07 – 0.40	2.82
Burnt [yes]	0.33 ***	0.22	-1.11	0.21 – 0.51	-1.54 – -0.67	-4.98
#Fires	1.28 *	0.10	0.24	1.05 – 1.55	0.05 – 0.44	2.43
aTCTwet_IQR * Burnt [yes]	0.86	0.11	-0.15	0.70 – 1.07	-0.36 – 0.06	-1.37

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

**Best model 11: Marginal R<sup>2</sup> = 0.426**

<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>std. Beta</i>	<i>CI</i>	<i>standardized CI</i>	<i>Statistic</i>
(Intercept)	7.81 ***	0.13	2.06	6.01 – 10.15	1.79 – 2.32	15.38
aPREC_SUM	1.22 ***	0.06	0.20	1.09 – 1.37	0.09 – 0.32	3.39
aTCTwet_IQR	1.14 *	0.06	0.13	1.02 – 1.29	0.02 – 0.25	2.23
Burnt [yes]	0.42 ***	0.16	-0.88	0.30 – 0.57	-1.19 – -0.56	-5.41
TSF	1.20 ***	0.05	0.18	1.08 – 1.34	0.08 – 0.29	3.38

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

**Table S4.** Model ranking of the variables that better explain *Psammodromus algirus* abundance in burnt plots at two megafires from Valencia province (E Iberian Peninsula). Lizard sampling was conducted during four years after the fire. The ranking was based on AICc values and only models with  $\Delta$  AICc < 2 are considered. Each row represents a model, and includes a description of the parameters and the variables used. Codes are the same as in Table S1. VIF – (Maximum) Variance Inflation Factor.

Model	df	AICc	$\Delta$ AICc	AICc weight	mR <sup>2</sup>	VIF	Model description
1	5	367,208	0,000	0,092	0,170	1.02	#Fires, aLST-Q50,
2	6	367,294	0,086	0,088	0,193	1.07	#Fires, aLST-Q50, aTCTbri_Q05,
3	7	367,571	0,363	0,076	0,207	2.57	#Fires, aLST-Q50, aLST_Q95, aTCTgrn_IQR,
4	6	367,641	0,433	0,074	0,185	1.08	#Fires, aLST-Q50, aTCTbri_IQR,
5	6	367,670	0,462	0,073	0,186	1.16	#Fires, aLST-Q50, aLST_Q95
6	6	368,257	1,049	0,054	0,178	1.07	#Fires, aLST-Q50, aTCTwet_IQR
7	8	368,356	1,147	0,052	0,232	2.77	#Fires, aLST-Q50, aLST_Q05, aLST_Q95, aTCTgrn_IQR,
8	6	368,372	1,163	0,051	0,190	1.31	#Fires, aLST-Q50, aLST_Q05,
9	8	368,451	1,243	0,049	0,212	5.59	#Fires, aLST-Q50, aLST_Q95, aTCTgrn_IQR, aTCTgrn_Q95,
10	6	368,592	1,383	0,046	0,183	1.11	#Fires, aLST-Q50, aPREC,
11	7	368,672	1,464	0,044	0,202	1.63	#Fires, aLST-Q50, aTCTbri_Q05, aTCTgrn_IQR,
12	8	368,699	1,491	0,044	0,216	2.96	#Fires, aLST-Q50, aLST_Q95, aNDVI_IQR, aTCTgrn_IQR,
13	6	368,761	1,553	0,042	0,175	1.36	#Fires, aLST-Q50, aNDVI_IQR,
14	7	368,975	1,766	0,038	0,206	1.39	#Fires, aLST-Q50, aLST_Q05, aTCTbri_Q05,
15	7	368,991	1,782	0,038	0,204	1.33	#Fires, aLST-Q50, aLST_Q05, aTCTbri_IQR,
16	7	369,079	1,871	0,036	0,206	3.10	#Fires, aLST-Q50, aTCTgrn_IQR,
17	5	369,096	1,888	0,036	0,127	1.01	aLST-Q50, aPREC, aTCTbri_IQR,
18	6	369,192	1,984	0,034	0,177	1.57	#Fires, TSF, aLST-Q50,
19	6	369,193	1,984	0,034	0,176	1.79	#Fires, aLST-Q50, aTCTgrn_Q95

**Table S5.** Model ranking of the variables that better explain *Psammodromus edwardsianus* abundance in unburnt and burnt plots at the Andilla megafire from Valencia province (E Iberian Peninsula). Lizard sampling was conducted during four years after the fire. The ranking was based

on AICc values and only models with  $\Delta AICc < 2$  are considered. Each row represents a model, and includes a description of the parameters and the variables used. Codes are the same as in Table S1. VIF: Variance Inflation Factor.

Model	aLST_Q05	aLST_Q50	aTCTbri_Q05	aTCTgrn_IQR	aTCTwet_IQR	Burnt	Elev	aTCTwet_IQR *Burnt	R <sup>2</sup> M	R <sup>2</sup> C	VIF	df	AICc	delta	weight
1					1.565	+	2.424	+	0.172	0.182	9.420	6.000	91.275	0.000	0.270
2			0.477		1.539	+	2.518	+	0.177	0.177	9.926	7.000	91.431	0.157	0.249
3	-0.196				1.633	+	2.564	+	0.182	0.193	9.708	7.000	92.827	1.552	0.124
4				0.334	1.603	+	2.525	+	0.177	0.182	9.741	7.000	92.830	1.555	0.124
5		-0.573	0.733				1.906		0.195	0.195	1.732	5.000	92.879	1.604	0.121
6		-0.424	0.589		0.262		2.073		0.178	0.178	1.821	6.000	93.038	1.764	0.112

**Figure S4:** (a) Abundance of *Psammodromus edwardsianus* along the four sampling years in relation to Fire condition (unburnt vs burnt plots). In Andilla. Boxes indicate the 25, 50% (median) and 75% quartiles, and lines show minimum and maximum values excluding outliers. (b) Ranking of the importance of explanatory variables considered to model *Psammodromus edwardsianus* abundance in Andilla. Analyses included unburnt and burnt plots, and variable names are as in Table S2.

