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Research article

Fire favors sexual precocity in a Mediterranean pine

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Wildfires are a natural disturbance in many ecosystems. Consequently, plant species have acquired traits that allow them to resist and regenerate in an environment with recurrent fires. A key trait in fire-prone ecosystems is the age at first reproduction (maturity age); populations of non-resprouting species cannot persist when the fire interval is shorter than this age. Maturity age is variable among individuals, so we hypothesized that short fire intervals select for early seed production (precocity). We selected 13 plots with different fire regimes in eastern Spain, all dominated by *Pinus halepensis* (a non-resprouting serotinous pine species). Then, we evaluated the age at first reproduction and the size of the canopy seed bank of each individual tree. Our results show a significant effect of fire regime on the onset of reproduction in this species, suggesting a selection towards higher precocity in populations subject to shorter fire intervals. Due to this higher precocity, pines stored more cones and therefore, increased their potential for reproduction post-fire. We provide the first field evidence that fire can act as a driver of precocity. Being precocious in fire-prone environments is adaptive because it increases the probability of having a significant seed bank when the next fire arrives.

Keywords: evolutionary ecology, fire traits, global change, maturity age, *Pinus halepensis*, serotiny

Introduction

Fires and plants have interacted for millions of years, generating evolutionary feedbacks (Pausas and Keeley 2009, Archibald et al. 2018). As a consequence, many plant species have acquired traits that enhance their fitness in environments with recurrent fires (He et al. 2011, Keeley et al. 2011, Pausas 2015, Lamont et al. 2019). There is now a bulk of evidence at the microevolutionary scale suggesting that particular fire regimes select for specific plant traits (Pausas et al. 2012, Hernández-Serrano et al. 2013, Vandvik et al. 2014).

Global change factors, including increased ignitions, land use changes and global warming, are changing fire regimes (e.g. reducing the interval of intense crown-fires) beyond the local historical variability (Enright et al. 2015, Turner et al. 2019, Pausas and Keeley 2021). For non-resprouting species, if the time needed for saplings to mature and begin to produce seeds is greater than fire interval (i.e. severe fires occur

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before sexual maturity), populations will fail to regenerate after fire. That is, a very short fire interval may strongly reduce population size of non-resprouting species or even lead them to local extinction (immaturity risk; Zedler et al. 1983, Keeley et al. 1999, Enright et al. 2015, Turner et al. 2019). Thus, sexual precocity (i.e. reproduction at an earlier age) is a key trait for persistence in a world with increasing fire activity. This is especially relevant for serotinous species, whose strategy to withstand fires is to accumulate a canopy seed bank in woody structures (cones or fruits) until the heat of a fire opens the cones and releases the seeds (Lamont et al. 2020). Thanks to this accumulation of seeds, serotinous species massively recruit in post-fire conditions where resource availability is high and competition is low (Causley et al. 2016, Lamont et al. 2020). However, serotiny is adaptive only when fire return intervals fall between the age of reproductive maturity and the plant's lifespan (Pausas and Keeley 2014, Lamont et al. 2020).

Several studies have highlighted the extraordinary importance of serotiny and precocity in post-fire population recovery, especially in pine species (Panetsos 1981, Daskalakou and Thanos 1996, Keeley and Zedler 1998, Tapias et al. 2001). The correlated evolution of serotiny and precocity and its relationship with the fire regime is also well documented in pines (Schwilk and Ackerly 2001). However, while most of the studies focus on interspecific variability of these reproductive traits, few consider intraspecific variability (Climent et al. 2008, Espelta et al. 2008, Santos-del-Blanco et al. 2010, 2013). There is sound evidence that the frequency of crown-fires increases the level of serotiny among populations of the same species (Gauthier et al. 1996, Radeloff et al. 2004, Hernández-Serrano et al. 2013). In the same way, the mechanism proposed to explain the evolution of precocity is the reduced fire interval (Keeley and Zedler 1998, Tapias et al. 2001, Climent et al. 2008); but to our knowledge, the effect of fire on the intraspecific variability of precocity has not yet been evaluated.

There is large variation (5–50 years) in the age at the first reproduction across pine species; those inhabiting fire-prone environments are more precocious than those from low productivity ecosystems that do not burn (deserts and high mountains; Keeley and Zedler 1998). There is also evidence of variability among and within populations (Supporting information; Turner 1985, Tapias et al. 2001, Ne'eman et al. 2004, Landis et al. 2005, Climent et al. 2008) and of high genetic control of precocity (Cecich et al. 1994, Santos-del-Blanco et al. 2010, Zhuk and Goroshkevich 2018). The fact that there is variability in precocity among populations could indicate different selection processes, while within population variability and heritability provides the opportunity for the evolution of this trait. Thus, we hypothesize that under short fire interval, only precocious trees will be able to produce seeds for recruiting after the second fire, with the consequent increase in precocity in the next generation. This selective pressure should be especially evident in non-resprouting serotinous species, including several pines, and should operate simultaneously with the observed reduction of post-fire tree density (Eugenio et al. 2006, Espelta et al. 2008). We predict that in these pine species, young trees from populations inhabiting environments where crown-fires are frequent will tend to reproduce earlier, thereby increasing the number of stored cones in comparison to those that inhabit environments that rarely burn. This, together with a higher level of serotiny, will allow individuals living in environments with recurrent fires to accumulate a larger canopy seed bank at early ages (Fig. 1) ensuring their reproduction post-fire. We tested this hypothesis in the widespread Mediterranean Aleppo pine *Pinus halepensis*.

Material and methods

Study species

Pinus halepensis is one of the most abundant and widespread tree species in the Mediterranean basin and it is dominant in the eastern Iberian Peninsula (Quézel 2000). The great regeneration capacity of *P. halepensis* is due to its reproductive precocity (Panetsos 1981), its large annual crop of cones and its ability to store serotinous cones in the canopy (Daskalakou and Thanos 1996). In the eastern Iberian Peninsula, this species occupies habitats with different frequencies of crown-fires and exhibits high variability in serotiny (Hernández-Serrano et al. 2013). Little is known about the degree of variation of precocity for this species as in most studies (Tapias et al. 2001, Climent et al. 2008) the mean age at first reproduction, which is estimated for even-aged populations, is based on the reproductive individuals only (a proportion of the entire population). Thus, this estimation is contingent on the age of the population (e.g. young populations with a few reproductive individuals will be considered more precocious than older populations). However, from those studies, we can infer that there is variability in this trait within and among populations. Furthermore, this species shows significant heritability in reproductive traits (flower and cone production; Matziris 1997), including precocity (Santos-del-Blanco et al. 2010). These characteristics make *P.*

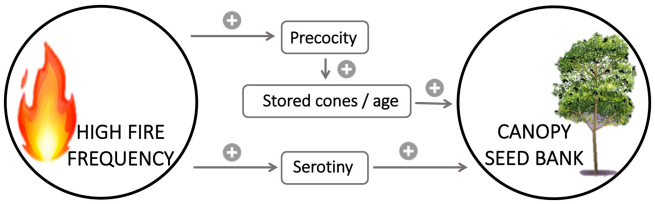


Figure 1. Conceptual diagram of the hypothesized mechanisms that modulate the size of the canopy seed bank in young pine trees. High frequency of fire selects for precocious individuals. As a result of precocity, these individuals store more cones at a given age than those who begin to reproduce later. Fire frequency also increases the level of serotiny, as the most serotinous individuals are more likely to reproduce after each fire. These two fire-mediated traits allow individuals growing in areas under high fire activity to increase the size of the canopy seed bank, and therefore improve their fitness after a fire.

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halepensis a good species model to test the influence of fire in shaping precocity variability.

Study sites and sampling

We selected 13 sites dominated by *P. halepensis* trees in the Valencia region (eastern Spain). In this area, crown-fires are more frequent at lower (warmer) altitudes (Verdú and Pausas 2007, Pausas and Verdú 2008, Hernández-Serrano et al. 2013); thus, to ensure the sampling includes variability in the fire regime, sites were selected across a range of altitudes (60–850 m approx.; Supporting information) and climatic conditions (Table 1). We used local forestry maps to confirm the dominance of young trees in each site and to avoid plantations. Distances between sites ranged from 6.1 to 165 km (77.5 ± 38.1 km, mean ± SD). In each site, we established four transects, spaced by at least 100 m. In each transect, we haphazardly selected and georeferenced 10 trees (40 trees per site, except S11 with 37 trees; Supporting information), separated by at least 10 m. Since tree size and conspecific density can affect cone production (Shmida et al. 2000, Niklas and Enquist 2003, Espelta et al. 2008, Strauss et al. 2017), we measured the basal diameter (10 cm above ground) of each tree and its distance to the two closest trees. We then calculated the annual growth rate as the basal diameter (cm) divided by the age (years) and the average of the distances to the two closest trees (hereafter, average distance). We estimated the age of each tree by counting whorls (Lamont 1985). Generally, *Pinus* species produce one whorl per year, but *P. halepensis* can produce several shoots annually. Therefore, this method to age the trees requires detecting whorls produced in the same year. Through field observations, we found that the secondary whorls have fewer and thinner branches and/or are closer to other whorls from the same growing season (see the Supporting information for more details). We validated this age estimation in post-fire stands in which the age of the regenerating trees is known (i.e. the time since the last crown-fire). For reproductive trees, we also estimated the age of each cone following the same method of counting whorls (avoiding immature cone cohorts; i.e. the last or last two cohorts depending on the sampling season) and recorded whether they were open (non-serotinous), closed (serotinous cones) or from the last cohort considered (closed but serotiny unknown). *Pinus halepensis* is a very flammable species that retains old branches and empty cones; they act as ladder fuels that carry the fire to the crown (Supporting information; Ne'eman and Arianoutsou 2021). This retention of branches and cones allowed us to estimate the age of the young tree and its cones (even if they were open), and therefore the age at first reproduction and the total number of stored cones (i.e. closed cones; an estimation of the canopy seed bank) for each tree. Field evidence suggested that some lower (thin) branches can be dropped at about the age of 20-year-old, thus, to avoid sampling errors, we established 18-year-old as the maximum age of the sampling individuals. Note that *P. halapensis* (like many other pines) starts reproducing as female. Also, pollen is unlikely to be limiting as this species produces an abundance of wind-dispersed pollen and forms extensive populations (Ne'eman et al. 2004). Thus, female cones are a good indicator of the first reproduction in this species.

Table 1. Fire activity index (FAI; standardized values of log-transformed sum of the fire sizes recorded in a 10 km radius circle surrounding each sampled site) and climate (mean annual precipitation and temperature, and aridity index), of the studied sites. Note that a lower aridity index value corresponds to more arid conditions. Additional details of the sites are given in the Supporting information.

Site code	FAI	Precipitation (mm)	Temperature (°C)	Aridity index
S1	1.00	560.15	15.33	0.283
S2	0.91	828.26	18.35	0.236
S3	0.87	558.50	16.36	0.270
S4	0.83	518.60	16.26	0.271
S5	0.73	569.60	15.69	0.311
S6	0.54	433.35	14.78	0.241
S7	0.52	526.82	17.55	0.290
S8	0.47	504.15	11.27	0.261
S9	0.40	427.77	12.6	0.240
S10	0.31	504.15	11.27	0.240
S11	0.26	563.79	11.04	0.284
S12	0.14	447.68	13.22	0.269
S13	0.00	421.75	14.47	0.233

Fire and climate characterization

The fire records available for our study region cover a period of 37 years (maps provided by the regional government of Valencia and Castilla la Mancha, from 1979 to 2016). Although there is evidence of overlapping fires with short intervals in our region (in relation to the longevity of the species; Malak and Pausas 2006, Malak et al. 2015), the fire return intervals in *P. halepensis* forest are considered to be in the order of decades (Naveh 1990, Agee 1998, Rundel et al. 2016). Then, the available fire data are too short to accurately depict the fire history of specific sites (i.e. at sampled-site scale) and particularly, to detect the occurrence of the less frequent events of overlapping fires with shorter intervals that promotes precocity. In addition, crown-fires in these forests are very intense and kill all individuals (stand-replacing fires), and therefore counting fire scars in the trunk is not an option in our study system. Thus, it is impossible to have reliable information on the specific fire recurrence and interval at the site scale. One way to overcome this lack of data is to estimate the fire regime for a larger area than the sites (i.e. the area surrounding the sites), obtaining more information from the available fire records. The area surrounding the sites can be considered similar to them in regard to their fire-proneness. Thus, using relatively large areas allows for estimating some long-term fire regime parameters, even with relatively short fire data (Hanes et al. 2019, Pausas 2022). That is, sites in areas with recent high fire activity are in more fire-prone environments and thus, they are more likely to have suffered recurrent (overlapping) fires with short fire intervals than sites located in areas with low fire activity in the last 37 years (less fire-prone). Specifically, we calculated a fire activity index (hereafter FAI) as the log-transformed sum of the sizes of all

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fires (i.e. cumulative burned area) recorded in the area of a 10 km radius circle surrounding each sampled site (i.e. buffer zone; see the Supporting information for further details); the value was then standardized between 0 and 1 (Table 1). The full size of each fire was included even if their areas exceeded the buffer zone. This FAI can be considered a proxy for the fire return interval at local (sampled-site) scale, as the higher the FAI, the greater the probability for any site to have experienced two consecutive fires with a short fire interval (because of the higher chance of fires to overlap). In addition, sites with high values of FAI are in more lowlands with warmer and dryer climates, corroborating the relationship between FAI and fire-proneness (Verdú and Pausas 2007, Pausas and Verdú 2008, Hernández-Serrano et al. 2013).

FAI values were computed using QGIS ver. 3.16.13 (QGIS Development Team 2019), by setting the 10 km buffer zones around our sites and intersecting with the fire maps. Note that all fire events were wildfires; prescribed burns were not performed in the region during the study period.

Another possible index of fire activity with the available fire records would be just the number of fires in the 10 km buffer zone, instead of cumulative burned area. In our sites the number of fires and cumulative burned area are correlated ($r = 0.89$, $p \leq 0.001$), indicating that sites with a higher burned area have also had more fires and therefore, high values of FAI are not conditioned by unusual events (i.e. a single large fire). We selected cumulative burned area for the analysis because it should be a better indicator of the fire return interval at the site scale as it accounts for the fire size (for the same number of fires, smaller fires are less likely to overlap than large fires), but results with the number of fires as a predictor variable are also presented in the Supporting Information.

To characterize the climate of our sites, we extracted mean annual temperature and mean annual precipitation (1951–2015 period) from a gridded map (0.1° resolution) provided by the Santander Meteorology Group (Herrera et al. 2012, 2016; Table 1). We also obtained aridity values from the Global Aridity Index map (30 arc-seconds resolution for the 1970–2000 period) (Trabucco and Zomer 2019; Table 1).

Statistical analyses

Before conducting our analyses, we tested the influence of FAI on average distance and growth rate, by fitting linear mixed models with site as random factor. FAI was not significant in explaining the differences in either average distance nor in growth rate (Supporting information).

To evaluate the role of fire regimen on per-individual age at first reproduction (precocity), we fitted a Cox proportional hazards regression model with the 'coxme' package (Therneau 2019). We used this survival analysis framework to account for censored data, i.e. to include individuals that did not reach sexual maturity at the sampling time. We included FAI as a predictor variable and site as a random factor. Given that cone production could also vary with tree size, tree density and climate, we added annual growth rate, average distance and the three climatic variables described above as covariates in the model. We also tested the interactions between FAI and the covariates.

To test whether the number of closed cones (as a proxy of the canopy seed bank) at the individual level differed depending on the FAI, we used a generalized linear mixed model (GLMM) with a Poisson error distribution and the log link function using the 'lme4' package (Bates et al. 2015). We included FAI as a predictor variable, and the same covariates as in the previous model, including for this model the age of the tree at sampling time. Then, to explore the influence of precocity in the number of closed cones accumulated in the canopy, we fitted a GLMM with the same structure, but added the number of years since the first reproductive event (maturity) as a predictor. The last variable removes the effect of precocity, and thus allows us to test whether the differences in the amount of cones are related to fire, independent of precocity. Failing to find a significant relation with fire in this latter model (and a significant effect in the previous) would suggest that precocity is a more relevant factor. For these two models we considered individual nested within site as random factor. We included an individual-level random effect to deal with overdispersion (Harrison 2014). Non-reproductive individuals and open cones do not contribute to the seed bank and thus were not considered in the analysis.

We used the 'ggeffects' package (Lüdecke 2018) to compute the predicted values of precocity and accumulated closed cones for the 75th and 25th percentile of the FAI values (i.e. for high and low fire activity, respectively). Given that the 'coxme' package used for the precocity model does not provide methods for obtaining conditional predicted values, we used the 'survival' package (*coxph* function; Therneau 2015) to obtain the predicted values of the probability of maturity. Both fitting methods (*coxme* and *coxph*) allow the inclusion of a random effect term and therefore, both methods are appropriate for the analysis. We prioritized *coxme* to test the model because it appears to be the most accurate when modeling mixed effects (Therneau 2015), but results with *coxph* are also presented (in the Supporting Information). In survival analyses, we calculate the probability of reaching sexual maturity as: $1 - P$, where P is the probability of being immature. All analyses were performed in R ver. 3.6.1 (www.r-project.org).

Results

Growth rate is the single variable that best explains precocity (positive relationship; Table 2a). Once we take into account growth rate, FAI is highly significant and positively related to precocity (Table 2a, Fig. 2a). Individuals growing in sites that frequently burn (75th percentile in the FAI frequency distribution) reach the 0.5 probability of being reproductive at 9 years old, while for individuals growing in sites that rarely burnt (25th percentile in the FAI) this probability is not reached until 13 years old (Fig. 2a). The relationship between average distance to closest trees and precocity was also significant and showed a negative tendency, that is, the more isolated individuals, the later they reached sexual maturity (Table 2a).

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Table 2. Results of the model for (a) precocity, (b) number of closed cones (proxy of the canopy seed bank) and (c) influence of precocity in the number of closed cones in relation to fire activity (FAI) and covariates (sequential addition of variables). Degree of freedom (df), log-likelihood (LogLik), $\chi 2$ and the associated p value of each step in the models are presented (**p < 0.01; ***p < 0.001). The last two columns provide the estimated coefficients and standard errors (SE) for the intercept (null model row) and fixed effects of the final model. Note that Cox models do not fit the intercept.

Model	df	LogLik	χ^2	p	Estimate	SE
(a) Precocity (Cox model)						
Null	3	−1460.4				
Growth rate	4	−1435.5	49.77	< 0.001***	0.32	0.04
+ Average distance	5	−1431.4	8.24	0.004**	−0.07	0.02
+ FAI	6	−1427.3	8.21	0.004**	0.44	0.13
(b) Number of closed cones (GLMM)						
Null	3	−832.49			−3.16	0.41
Growth rate	4	−793.92	77.15	< 0.001***	0.27	0.03
+ Age	5	−768.81	50.22	< 0.001***	0.19	0.02
+ FAI	6	−763.08	11.46	< 0.001***	0.13	0.03
(c) Precocity influence in the number of closed cones (GLMM)						
Null	3	−832.49			−2.96	0.44
Growth rate	4	−793.92	77.15	< 0.001***	0.26	0.02
+ Age	5	−768.81	55.22	< 0.001***	0.13	0.02
+ Years since maturity	6	−756.42	24.78	< 0.001***	0.11	0.02
+ Temperature	7	−750.72	11.41	< 0.001***	0.08	0.02

The number of closed cones was significantly and positively related to the growth rate and the age of the tree (Table 2b). Once these two variables were included in the models, FAI was still significant (Table 2b, Fig. 2b), indicating that the trees bear more cones in sites with higher FAI. However, when we include the number of years since maturity, this variable was significant in explaining the differences in the number of closed cones (and FAI was no longer significant; Table 2c). Of the other covariates included in the model, only mean annual temperature contributed to explaining the number of closed cones (positive relationship; Table 2c). That is, more precocious trees showed more stored cones at a given tree age, regardless of fire activity. In other words, the main mechanism by which fire increases the number of stored cones at a given age (Table 2b) is by increasing precocity (Table 2a) and not by other fire-related processes (e.g. higher productivity post-fire; Table 2c).

All these results are independent of the fitting method (Supporting information) and the logarithmic transformation (Supporting information). In addition, the results are basically the same if we use the number of fires instead of FAI as a predictor variable (Supporting information).

Discussion

There is a positive relationship between fire activity experienced by the population and the onset of reproduction in *P. halepensis* trees (Table 2a). Because populations in more fire-prone habitats (high FAI) likely suffered more recurrent (overlapping) fires, our results suggest that the increase in precocity may be driven by short fire intervals. Previous studies have shown significant heritability of precocity (Santos-del-Blanco et al. 2010) and have proposed fire as a likely driver for the evolution of this trait in *P. halepensis* (Tapias et al. 2001, Climent et al. 2008). Taken together, these results suggest that short fire intervals prevent the reproduction of slow reproducing individuals and thus, select the most precocious ones. To our knowledge, we provide the first field evidence of this phenomenon.

Furthermore, we found that fire activity increases the number of cones accumulated in the canopy at a given age (Table 2b), and that this effect is not explained by higher cone productivity of populations under high fire activity, but by their higher precocity (Table 2c). This result is consistent with precocious individuals bearing more cones in homogeneous growing conditions (common gardens experiments; Santos-del-Blanco et al. 2010). Since we only considered cones that were closed at the sampling time, an alternative explanation for the observed differences could be the opening of the cones. However, the serotiny degree (proportion of closed cones respect to the total) is very high in young *P. halepensis* trees (Tapias et al. 2001, Ne'eman et al. 2004). In fact, in our study, open cones accounted for only 8% of the total sampled cones (n = 2193) and we found no evidence that fire activity or any of the covariates considered affected cone opening (Supporting information). Accordingly, precocious individuals bear more cones at a given age (compared to individuals that begin to reproduce later), and thus it is likely that they accumulate a larger canopy seed bank at young ages. In pines, the number of seeds per cone may show some variability across cones and trees, but there is no evidence that they vary with fire activity. Thus, the observed differences in the number of cones suggest a different size of the seed bank. The consequence is that trees subject to high fire activity are more likely to reproduce and leave more offspring if the next fire comes after a short period. The fact that precocity and serotiny are correlated traits among pine species (Schwilk and Ackerly 2001) suggests that this process is likely to be quite general in serotinous species. Our results also add further evidence to the role of fire in shaping intraspecific variability in plant traits (Gómez-González et al.

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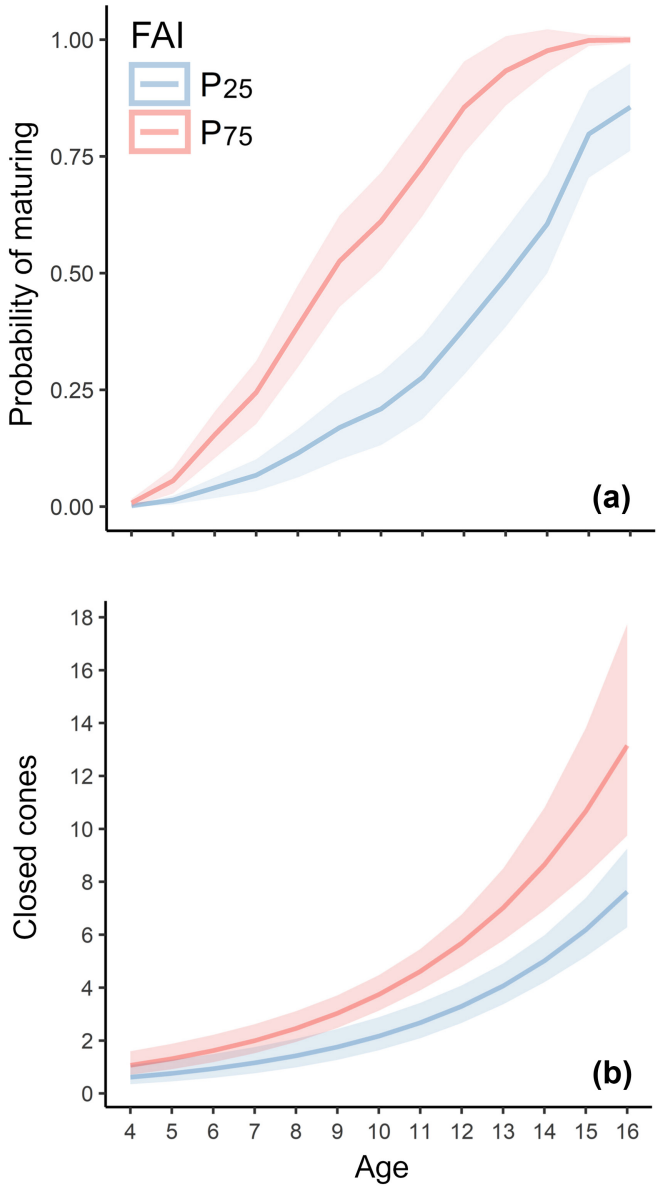


Figure 2. Fitted lines for 75th (in red; upper lines) and 25th (in blue; lower lines) percentile of fire activity index (FAI; i.e. high and low fire activity) for the models relating (a) probability of reaching sexual maturity (precocity; Supporting information), and (b) number of closed cones (proxy of the canopy seed bank; Table 2b) against the age of the individuals. Shaded area shows the confidence intervals. Note that in precocity models (Supporting information) age is not included as a predictor since Cox models use time to event (i.e. age) as a response variable.

2011, Pausas et al. 2012, Hernández-Serrano et al. 2013, Vandvik et al. 2014).

Pinus halepensis saplings with a higher growth rate exhibited higher precocity (Table 2a). Tree size (represented by age, and for a given tree cohort, by growth rate) also influenced cone production (Table 2b), and this effect was significant even when we take into account the effect of precocity (Table 2c). This positive relationship between growth and reproductive investment (precocity and cone production) has been widely documented in pines (Shmida et al. 2000, Niklas and Enquist 2003, Espelta et al. 2008). In common garden experiments, however, some authors have observed a tradeoff between investment in reproduction and vegetative growth in pines, with a maximum allocation to reproduction in middle-size individuals (Climent et al. 2008, Santos-del-Blanco et al. 2010). These contrasting results could be explained by the spatial heterogeneity in natural environments, supported by the higher growth rate variability within than among sites in our data (76% and 24%, respectively). This heterogeneity gives individuals different access to resources, which can blur the reproduction–growth tradeoffs (Reznick et al. 2000).

Previous studies have revealed the negative effects of tree density on reproduction, either due to competition for soil resources or due to the interference between crowns, which limits light and wind pollination (Strauss et al. 2017). However, most of the studies evaluating the effects of density have been conducted in experimentally thinned plots (González-Ochoa et al. 2004, Verkaik and Espelta 2006), so small-scale effects of spatial heterogeneity in the distribution of individuals were not taken into account. We found that the most isolated individuals (within the sampled site) showed a later onset of reproduction (Table 2a). Since this result is not due to different resource allocations (differences in growth have already been taken into account), it could be a signature of the seed shadow from the mother trees. Post-fire recruitment normally occurs close to the mother tree, generating a spatial genetic structure of the population (Ayre et al. 2010, Hernández-Serrano et al. 2013). Therefore, is likely that after a second fire, precocious mothers will leave a more profuse offspring (because of a larger seed bank), while less precocious mothers will leave a fewer and more dispersed offspring. This could explain the observed pattern, although we cannot address this in detail with the available data. Overall our results emphasize the importance of field-based studies to understand ecological processes.

Although a high frequency of fires favors precocity, not all individuals are mature up to 16 years old (Table 2a, Fig. 2a). Thus, recurrent fires with fire intervals shorter than 16 years may reduce the density of the post-fire population, as it excludes slow-reproducing individuals and the canopy seed bank of the precocious ones may not be large enough to reach the pre-fire density. This is in line with previous studies showing that the minimum fire interval for *P. halepensis* populations to recover the pre-fire density level is 15 years (Eugenio et al. 2006, Espelta et al. 2008). The occurrence of such short fire intervals is currently anomalous in our region. However, fire activity is likely to increase in the study area as temperatures and rural depopulation increase and urban populations spread into the forest-urban interface (Pausas and Millán 2019). This tendency could compromise the persistence of *P. halepensis* populations, especially those growing in places with historically low fire activity (less precocious). That is, pine populations with histories of lower fire activity are more sensitive to abrupt increases in fire frequency. In short, to what extent the lower density of precocious trees will maintain the population is beyond the objectives of this paper and requires further research; but will likely depend

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on the interplay between the number of recurrent fires, their interval and the precocity of the population, together with other characteristics of the site (Pausas et al. 2004).

In conclusion, our study suggests that fire can act as a driver of precocity in serotinous species, and this implies that populations under high fire activity accumulate larger canopy seed banks at young ages. That is, being precocious in an environment that burns frequently has a high adaptive value, as it increases the probability of reproduction after a short fire interval. These results also have direct management implications; selecting seeds from populations with high fire activity for restoration projects would increase the resilience capacity of the restored woodland to face novel fire regimes with increased fire frequency (Leverkus et al. 2021). Our results provide evidence that there is room for the evolution of serotinous species to adapt to novel fire regimes, whenever the increase of fire activity remains under a certain limit. Furthermore, our results demonstrate significant variability in the sensitivity of population to fire regime changes.

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Author contributions

Carmen Guiote: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Methodology (equal); Writing – original draft (lead). **Juli G. Pausas**: Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Methodology (equal); Resources (lead); Supervision (lead); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xgxd254km (Guiote and Pausas 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Agee, J. K. 1998. Ecology and biogeography of *Pinus*. – In: Richardson, D. M. (ed.), Ecology and biogeography of *Pinus*. Cambridge Univ. Press, pp. 193–218.

Archibald, S., Lehmann, C., Belcher, C., Bond, W., Bradstock, R., Daniau A.-L., Dexter, K., Forrestel, E., Greve, M., He, T., Higgins, S., Hoffmann, W. A., Lamont, B., McGlinn, D., Moncreiff, G., Osborne, C., Pausas, J. G., Price, O., Ripley, B., Rogers, B., Schwilk, D., Simon, M., Turetsky, M., Van der Werf, G. and Zanne, A. 2018. Biological and geophysical feedbacks with fire in the earth system. – Environ. Res. Lett. 13: 033003.

Ayre, D., O'Brien, E., Ottewell, K. and Whelan, R. 2010. The accumulation of genetic diversity within a canopy-stored seed bank. – Mol. Ecol. 19: 2640–2650.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48. https://cran.r-project.org/web/packages/lme4/vignettes/lmer.pdf.

Causley, C. L., Fowler, W. M., Lamont, B. B. and He, T. 2016. Fitness benefits of serotiny in fire- and drought-prone environments. – Plant Ecol. 217: 773–779.

Cecich, R. A., Kang, H. and Chalupka, W. 1994. Regulation of early flowering in *Pinus banksiana*. – Tree Physiol. 14: 275–284.

Climent, J., Prada, M. A., Calama, R., Chambel, M. R., de Ron, D. S. and Alía, R. 2008. To grow or to seed: ecotypic variation in reproductive allocation and cone production by young female Aleppo pine (*Pinus halepensis*, Pinaceae). – Am. J. Bot. 95: 833–842.

Daskalakou, E. N. and Thanos, C. A. 1996. Aleppo pine (*Pinus halepensis*) postfire regeneration: the role of canopy and soil seed banks. – Int. J. Wildland Fire 6: 59–66.

Enright, N. J., Fontaine, J. B., Bowman, D. M. J. S., Bradstock, R. A. and Williams, R. J. 2015. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. – Front. Ecol. Environ. 13: 265–272.

Espelta, J. M., Verkaik, I., Eugenio, M. and Lloret, F. 2008. Recurrent wildfires constrain long-term reproduction ability in *Pinus halepensis* Mill. – Int. J. Wildland Fire 17: 579–585.

Eugenio, M., Verkaik, I., Lloret, F. and Espelta, J. M. 2006. Recruitment and growth decline in *Pinus halepensis* populations after recurrent wildfires in Catalonia (NE Iberian Peninsula). – For. Ecol. Manage. 231: 47–54.

Gauthier, S., Bergeron, Y. and Simon, J. P. 1996. Effects of fire regime on the serotiny level of jack pine. – J. Ecol. 84: 539–548.

Gómez-González, S., Torres-Díaz, C., Bustos-Schindler, C. and Gianoli, E. 2011. Anthropogenic fire drives the evolution of seed traits. – Proc. Natl Acad. Sci. USA 108: 18743–18747.

González-Ochoa, A. I., López-Serrano, F. R. and De Las Heras, J. 2004. Does post-fire forest management increase tree growth and cone production in *Pinus halepensis*? – For. Ecol. Manage. 188: 235–247.

Guiote, C. and Pausas, J. G. 2022. Data from: Fire favors sexual precocity in a Mediterranean pine. – Dryad Digital Repository, https://doi.org/10.5061/dryad.xgxd254km.

Hanes, C. C., Wang, X., Jain, P., Parisien, M.-A., Little, J. M. and Flannigan, M. D. 2019. Fire-regime changes in Canada over the last half century. – Can. J. For. Res. 49: 256–269.

Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. – PeerJ 2: e616.

He, T., Lamont, B. B. and Downes, K. S. 2011. *Banksia* born to burn. – New Phytol. 191: 184–196.

Hernández-Serrano, A., Verdú, M., González-Martínez, S. C. and Pausas, J. G. 2013. Fire structures pine serotiny at different scales. – Am. J. Bot. 100: 2349–2356.

16000706, 2023, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/oik.09373 by Csic Organización Central Om (Oficialia Mayor) (Urici), Wiley Online Library on [27/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Herrera, S., Gutiérrez, J. M., Ancell, R., Pons, M. R., Frías, M. D. and Fernández, J. 2012. Development and analysis of a 50-year high-resolution daily gridded precipitation dataset over Spain (Spain02). – Int. J. Climatol. 32: 74–85.
Herrera, S., Fernández, J. and Gutiérrez, J. M. 2016. Update of the Spain02 gridded observational dataset for EURO-CORDEX evaluation: assessing the effect of the interpolation methodology. – Int. J. Climatol. 36: 900–908.
Keeley, J. E. and Zedler, P. H. 1998. Life history evolution in pines. – In: Richardson, D. M. (ed.), Ecology and biogeography of *Pinus*. Cambridge Univ. Press, pp. 219–242.
Keeley, J. E., Ne'eman, G. and Fotheringham, C. J. 1999. Immaturity risk in a fire dependent pine. – J. Mediterr. Ecol. 1: 41–48.
Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J. and Bradstock, R. A. 2011. Fire as an evolutionary pressure shaping plant traits. – Trends Plant Sci. 16: 406–411.
Lamont, B. B. 1985. Fire responses of sclerophyll shrubland – a population ecology approach, with particular reference to the genus *Banksia*. – In: Ford, J. (ed.), Ecology and management of fire in natural ecosystems of Western Australia. Environmental Studies Group, pp. 41–46.
Lamont, B. B., He, T. and Yan, Z. 2019. Evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. – Biol. Rev. 94: 903–928.
Lamont, B. B., Pausas, J. G., He, T., Witkowski, E. T. F. and Hanley, M. E. 2020. Fire as a selective agent for both serotiny and nonserotiny over space and time. – Crit. Rev. Plant Sci. 39: 140–172.
Landis, R. M., Gurevitch, J., Fox, G. A., Fang, W. and Taub, D. R. 2005. Variation in recruitment and early demography in *Pinus rigida* following crown fire in the pine barrens of Long Island, New York. – J. Ecol. 93: 607–617.
Leverkus, A. B., Thorn, S., Gustafsson, L., Noss, R., Müller, J., Pausas, J. G. and Lindenmayer, D. B. 2021. Environmental policies to cope with novel disturbance regimes – steps to address a world scientists' warning to humanity. – Crit. Rev. Plant Sci. 16: 021003.
Lüdecke, D. 2018. ggeffects: tidy data frames of marginal effects from regression. – J. Open Source Softw. 3: 772. https://cran.r-project.org/web/packages/ggeffects/ggeffects.pdf.
Malak, D. A. and Pausas, J. G. 2006. Fire regime and post-fire normalized difference vegetation index changes in the eastern Iberian peninsula (Mediterranean basin). – Int. J. Wildland Fire 15: 407–413.
Malak, D. A., Pausas, J. G., Pardo Pascual, J. and Ruiz, L. A. 2015. Fire recurrence and the dynamics of enhanced vegetation index in a Mediterranean ecosystem. – Int. J. Appl. Geospat. Res. 6: 18–35.
Matziris, D. 1997. Variation in growth, flowering and cone production in a clonal seed orchard of Aleppo pine grown in Greece. – Silvae Genet. 46: 224–228.
Naveh, Z. 1990. Fire in the Mediterranean – a landscape ecologicalperspective. – In: Goldammer, J. G. and Jenkins, M. J. (eds), Fire in ecosystems dynamics: Mediterranean and northern perspective. SPB Academic Publishing, pp. 1–20.
Ne'eman, G. and Arianoutsou, M. 2021. Mediterranean pines – adaptations to fire. – In: Ne'eman, G. and Osem, Y. (eds), Pines and their mixed forest ecosystems in the Mediterranean basin. Managing forest ecosystems, Vol. 38. Springer, pp. 457–480.
Ne'eman, G., Goubitz, S. and Nathan, R. 2004. Reproductive traits of *Pinus halepensis* in the light of fire – a critical review. – Plant Ecol. 171: 69–79.
Niklas, K. J. and Enquist, B. J. 2003. An allometric model for seed plant reproduction. – Evol. Ecol. Res. 5: 79–88.
Panetsos, K. P. 1981. Monograph of *Pinus halepensis* Mill. and *P. brutia* Ten. – Ann. For. 9: 39–77.
Pausas, J. G. 2015. Evolutionary fire ecology: lessons learned from pines. – Trends Plant Sci. 20: 318–324.
Pausas, J. G. 2022. Pyrogeography across the western Palearctic: a diversity of fire regimes. – Global Ecol. Biogeogr. 32: 1923–1932.
Pausas, J. G. and Verdú, M. 2008. Fire reduces morphospace occupation in plant communities. – Ecology 89: 2181–2186.
Pausas, J. G. and Keeley, J. E. 2009. A burning story: the role of fire in the history of life. – BioScience 59: 593–601.
Pausas, J. G. and Keeley, J. E. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. – New Phytol. 204: 55–65.
Pausas, J. G. and Millán, M. M. 2019. Greening and browning in a climate change hotspot: the Mediterranean Basin. – Bioscience 69: 143–151.
Pausas, J. G. and Keeley, J. E. 2021. Wildfires and global change. – Front. Ecol. Environ. 19: 387–395.
Pausas, J. G., Ribeiro, E. and Vallejo, R. 2004. Post-fire regeneration variability of *Pinus halepensis* in the eastern Iberian Peninsula. – For. Ecol. Manage. 203: 251–259.
Pausas, J. G., Alessio, G. A., Moreira, B. and Corcobado, G. 2012. Fires enhance flammability in *Ulex parviflorus*. – New Phytol. 193: 18–23.
QGIS Development Team 2019. QGIS Geographic Information System. – Open Source Geospatial Foundation Project, http://qgis.osgeo.org.
Quézel, P. 2000. Taxonomy and biogeography of Mediterranean pines (*Pinus halepensis* and *P. brutia*). – In: Ne'eman, G. and Trabaud, L. (eds), Ecology, biogeography and management of *Pinus halepensis* and *P. brutia* forest ecosystems in the Mediterranean Basin. Backhuys Publishers, pp. 1–12.
Radeloff, V. C., Mladenoff, D. J., Guries, R. P. and Boyce, M. S. 2004. Spatial patterns of cone serotiny in *Pinus banksiana* in relation to fire disturbance. – For. Ecol. Manage. 189: 133–141.
Reznick, D., Nunney, L. and Tessier, A. 2000. Big houses, big cars, superfleas and the costs of reproduction. – Trends Ecol. Evol. 15: 421–425.
Rundel, P. W., Arroyo, M. T., Cowling, R. M., Keeley, J. E., Lamont, B. B. and Vargas, P. 2016. Mediterranean biomes: evolution of their vegetation, floras and climate. – Annu. Rev. Ecol. Evol. Syst. 47: 383–407.
Santos-del-Blanco, L., Zas, R., Notivol, E., Chambel, M. R., Majada, J. and Climent, J. 2010. Variation of early reproductive allocation in multi-site genetic trials of Maritime pine and Aleppo pine. – For. Syst. 19: 381–392.
Santos-del-Blanco, L., Bonser, S. P., Valladares, F., Chambel, M. R. and Climent, J. 2013. Plasticity in reproduction and growth among 52 range-wide populations of a Mediterranean conifer: adaptive responses to environmental stress. – J. Evol. Biol. 26: 1912–1924.
Schwilk, D. W. and Ackerly, D. D. 2001. Flammability and serotiny as strategies: correlated evolution in pines. – Oikos 94: 326–336.
Shmida, A., Lev-Yadun, S. and Ne'eman, G. 2000. Sexual allocation and gender segregation in *Pinus halepensis*, *P. brutia* and *P. pinea*. – In: Ne'eman, G. and Trabaud, G. L. (eds), Ecology, biogeography and management of *Pinus halepensis* and *P. brutia* ecosystems in the Mediterranean Basin. Backhuys Publishers, pp. 91–104.

16000706, 2023, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/oik.09373 by Csic Organización Central Om (Oficialia Mayor) (Urici), Wiley Online Library on [27/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Strauss, S. H., Jones, K. N., Lu, H., Petit, J. D., Klocko, A. L., Betts, M. G., Brosi, B. J., Fletcher, R. J. and Needham, M. D. 2017. Reproductive modification in forest plantations: impacts on biodiversity and society. – New Phytol. 213: 1000–1021.

Tapias, R., Gil, L., Fuentes-Utrilla, P. and Pardos, J. A. 2001. Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. – J. Ecol. 89: 629–638.

Therneau, T. 2015. A package for survival analysis in R. – https://cran.r-project.org/web/packages/survival/vignettes/survival.pdf.

Therneau, T. 2019. Coxme: mixed effects cox models. – https://cran.r-project.org/web/packages/coxme/coxme.pdf.

Trabucco, A. and Zomer, R. J. 2019. Global aridity index and potential evapo-transpiration (ET0) climate database v2. – https://figshare.com/articles/dataset/Global_Aridity_Index_and_Potential_Evapotranspiration_ET0_Climate_Database_v2/7504448/3.

Turner, D. P. 1985. Successional relationships and a comparison of biological characteristics among six northwestern conifers. – Bull. Torrey Bot. Club 112: 421–428.

Turner, M. G., Braziunas, K. H., Hansen, W. D. and Harvey, B. J. 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. – Proc. Natl Acad. Sci. USA 166: 11319–11328.

Vandvik, V., Töpper, J. P., Cook, Z., Daws, M. I., Heegaard, E., Måren, I. E. and Velle, L. G. 2014. Management-driven evolution in a domesticated ecosystem. – Biol. Lett. 10: 20131082.

Verdú, M. and Pausas, J. G. 2007. Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. – J. Ecol. 95:1316–1323.

Verkaik, I. and Espelta, J. M. 2006. Post-fire regeneration thinning, cone production, serotiny and regeneration age in *Pinus halepensis*. – For. Ecol. Manage. 231: 155–163.

Zedler, P. H., Gautier, C. R. and McMaster, G. S. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. – Ecology 64: 809–818.

Zhuk, E. and Goroshkevich, S. 2018. Growth and reproduction in *Pinus sibirica* ecotypes from western Siberia in a common garden experiment. – New For. 49: 159–172.

16000706, 2023, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/oik.09373 by Csic Organización Central Om (Oficialia Mayor) (Urici), Wiley Online Library on [27/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License