


Post-fire Regeneration Traits of Understorey Shrub Species Modulate Successional Responses to High Severity Fire in Mediterranean Pine Forests

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ABSTRACT

Recurrent fires can impede the spontaneous recruitment capacity of pine forests. Empirical

studies have suggested that this can lead to a prolonged replacement of pine forest by shrubland, especially if shrub species are pyrophytic. Model-based studies, however, have suggested that post-fire succession of pine forest under current climatic conditions will eventually tend towards the dominance of oaks under high fire severity and recurrence. These previous modelling studies did not address the role of the various post-fire regeneration traits of the understorey shrub species. Considering the dichotomy of obligate seeder vs. resprouter species, either obligate or facultative resprouter, we hypothesized that when the shrubs present are post-fire seeders, the oaks steadily occupy the forest, whereas resprouter shrub species might compete with oaks and delay or arrest post-fire succession. To test this hypothesis, we developed a dynamic, cellular automaton model for simulating post-fire successional transitions in pine forests, including shrubs, pines and oaks, and stochastic fires of regular frequency. Our results

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showed a strong tendency towards oak dominance as final model state and a very reduced role of fire recurrence in this final state, with low yearly acorn input delaying oak dominance. Most relevantly, and in line with our hypothesis, the trend towards oak dominance depended markedly on the two types of shrub species, being delayed by resprouter species, which extended the shrub-dominated succession stage for several centuries. Our simula-

tion results supported the view that the type of understorey species should be a key consideration in post-fire restoration strategies aiming to enhance fire resilience.

Key words: facultative shrub species; obligate seeder shrub species; pine forests; arrested succession; mediterranean plant communities; cellular automata; wildfires; oak regeneration.

HIGHLIGHTS

- Oaks were dominant both in the absence of fire and under high fire recurrence.
- Post-fire regeneration was key, with facultative shrub species delaying succession.
- Understorey species regeneration type should be considered in post-fire restoration.

INTRODUCTION

In the past fifty years, Mediterranean landscapes experienced intense changes that led to abandonment of marginal croplands, on the one hand, and, on the other hand, to extensive afforestation with pine plantations (Pausas and others 2004a, b; Vallejo and others 2012a, b). These changes have contributed to intensifying fire regimes in the Mediterranean Basin, which in turn, can have pronounced effects on the composition and long-term resilience of its plant communities (Díaz-Delgado and others 2002; Vallejo and others 2012a, b).

According to the classical view on succession, species replacement in the absence of disturbance is driven by facilitation mechanisms, with early successional species creating conditions that are less favourable for themselves than for late successional species (Clements 1916; Connell and Slatyer 1977). In line with this theory, undisturbed Mediterranean pine forests are considered to foster successional processes, in particular by creating conditions under their canopy that are favourable for the establishment of late successional species (for example, *Quercus ilex*; Zavala and others 2000). Most Mediterranean plant species are well adapted to fire occurrence, responding to fire through three main regeneration strategies (also called plant functional types, PFT): (i) plant survival through the resistance of below-ground buds to fire, followed by resprouting of the above-ground tissues

(obligate resprouters), and recruitment is produced in the intervals between fires (Keeley and others 2012), (ii) plant mortality with survival of the seeds (obligate seeders) or (iii) a combination of both mechanisms [facultative shrub species; according to Pausas and others (2004a, b) and Paula and Pausas (2008)]. Studies of post-fire dynamics have shown that plant communities dominated by resprouter species (which are usually late successional) are more resilient to both short and long fire intervals than communities dominated by seeder species (Keeley 1986), yet important questions remain on how the various plant functional types interact in shaping the post-fire community development.

The resilience of pine forests to frequent fires is largely limited by pine seed production. This means that the occurrence of high recurrent repeated fires in a short interval of time or of a single fire in a young pine forest can cause the local eradication of pines (immaturity risk; Moreira and others 2011; De las Heras and others 2012). This eradication gives rise to the dominance of other species, which could either be early or late successional, depending on the species composition of the understory before the fire (Rodrigo and others 2004). In this context, several studies indicate that high wildfire frequency can favour the replacement of pine and oak forests by fire-prone shrublands (Acácio and others 2009, 2010; Santana and others 2010, 2014). Furthermore, the colonization of late successional species, such as resprouter oak trees, in fire-prone shrublands can be limited by several factors related to seed dispersal and micro-climate conditions (Acácio and others 2007; Pons and Pausas 2007). These recruitment limitations could arrest successional processes, locking the system in a shrubland state, that is, plant communities that lack a tree layer and are dominated by fire-prone shrub species (Acácio and others 2007, 2009, 2010; Santana and others 2010). The dominance of fire-prone shrublands can markedly reduce the resilience of the ecosystem by, for example, increasing erosion risk and decreasing biodiversity (Mayor

and others 2016; Van del Elsen and others 2020). Despite this, oak tree species can also become dominant in former pine forests where pines have been eradicated as a result of recurrent fires (Keelley 1986; Torres and others 2016; Baudena and others 2020).

Plant succession is expected to be modulated by factors such as fire severity (Díaz-Delgado and others 2003; López-Poma and others 2014), seed source, disperser preference, and the occurrence of safe germination microsites (Pons and Pausas 2006, 2007). The persistence of a litter layer after a fire, which largely depends on fire severity (Lamont and others 1993; Maia and others 2012), modifies the colonization probability of plants from different functional groups. Thick litter layers may selectively inhibit the germination and establishment of species with small seeds (Farrell and others 2012; Loydi and others 2013) as opposed to big seeds (Thompson 2000). This contrast in seed size broadly coincides with that in early versus late successional Mediterranean species and, simultaneously, with that between obligate seeder shrubs versus resprouter species (Cerabolini and others 2003). Also, by buffering temperature and moisture fluctuations, pine litter favours the establishment of late successional species over that of early successional species (Facelli and Pickett 1991; Gaudio and others 2011). However, despite the important role of litter as modulator of the composition and structure of plant communities (Xiong and Nilsson 1999), its effects have not been included so far in the analysis of the successional dynamics of pine forests under different fire regimes.

According to Baudena and others (2020), pine forests will be replaced by oak forests in the long run. However, the post-fire resprouting ability of oak trees can be hampered because of unfavourable environmental conditions, for example, due to the predicted climatic changes; this can, in turn, lead to the dominance of fire-prone shrublands instead of late successional oak forests. Furthermore, we expect that, under high fire recurrence, oak tree dominance will be delayed by reduced seed colonization (low seed entry). We hypothesise that facultative resprouter shrubs will likely delay oak tree dominance further than obligate seeder shrubs because facultative species exhibit both a positive fire feedback due to their high flammability and a high persistence after fire due to their resprouting capacity. In short, whereas frequent fires in a short interval can deplete seed banks of obligate seeder shrubs, facultative shrub species can persist by their resprouting capacity, thus delaying their replacement by late successional species. According to this

hypothesis, the main objective of this study was to improve our understanding of the role of facultative resprouter shrubs in delaying succession, represented by the dominance of oak tree species, following wildfire.

To test the role of shrubs in post-fire succession, we developed a dynamic successional model that simulates the population dynamics of three plant functional types simultaneously: pine, oak tree and either an obligate seeder or a facultative shrub species. The simulated temporal scale allowed species replacement and succession. Using this model, we studied the long-term vegetation dynamics of a mimicked Mediterranean pine forest under different understorey functional composition (obligate seeder versus facultative species) and fire frequency conditions, and we analysed the dynamics of the transient period (until approximately 1000 years), by studying the time at which the late successional species (oak tree) attained relative dominance. Additionally, we studied how the oak tree colonization capacity (represented by the entry of acorns) and post-fire microsite conditions (represented by fire severity and litter depth) influence the progress of succession.

MATERIAL AND METHODS

We implemented a stochastic cellular automata model (also called interacting particle systems; Durrett and Levin 1994), which allowed representing spatial processes at the landscape scale. Cellular automata consist of one lattice, in which each cell acquires a discrete and finite value, and of transition rules that control the temporal and spatial changes in the values of the state of the cells (Wolfram 1984). In our model, the state variable was the plant functional type. The lattice had 100*100 cells (each cell being denoted by x in what follows), and each cell contained only one plant type, which could be interpreted as one adult tree but also of few small shrub plants. For simplification purposes, if the cell was considered as occupied by more plants, they were of the same type and age. The model considered three plant types ($i=1-3$), each representing a different functional group with contrasting seed size, seed production and life span. Namely, we modelled pines ($i=1$), either facultative or obligate seeder shrubs ($i=2$) and oak tree ($i=3$). *Pines* are obligate seeder trees of intermediate lifespan that accumulate their seeds in aerial seedbanks by means of serotinous cones (Table 1). Seeder shrubs have a shorter life-span but a quicker age of maturity. Seeder shrubs regenerate after fire by means of seeds stored in a

Table 1. List of Symbols, Names, Values, Units, and their Source for the Parameters.

Symbol	Interpretation	Values in use for				
		Pine ($i=1$)	Shrub ($i=2$)	Oak ($i=3$)	Units	Sources ^{a,b,c}
SP_1	Annual seed production per cell	100	1000	10	Seeds. y^{-1}	<i>a</i>
DS	Degree of serotiny	0.5	–	–	–	<i>a</i>
lrate	Annual litter accumulation rate	0.8			cm y^{-1}	
AM	Age of maturity	10	2	20	y	<i>b</i>
E_i	Competition factor for the seedlings	10	100	2		–
AMOrate	Annual mortality rate	1/100	1/30	1/1000	y	<i>c</i>

^aGómez and others (2003) and Vega and others (2008).
^bFor *Pinus* spp.: Tapias and others (2001); Thanos and Daskalaku (2000); for oak: Pausas (1999a) and the authors, unpublished.
^cBaudena and others (2020).

soil bank. Shrub species could also be facultative seeders if they can both germinate and resprout after fire. Finally, oak trees are obligate resprouter trees. That is, this plant type only regenerates by resprouting after fire, while recruitment by seeds only occur in inter-fire periods (Pausas 1999a, b). Obligate resprouting shrubs (for example, *Quercus coccifera*, the only shrubby oak in the Mediterranean Europe) is not considered in this work. For the pine plant type, the model species were inspired in *Pinus pinaster* Ait. For shrubs, the model species were inspired in *Genista* spp. (including formerly classified *Pterospartum tridentatum* (L.) Willk.), *Erica australis* L. and *Ulex europaeus* L. for the facultative species, while for obligate seeder species, we considered *Erica umbellata* L., *Ulex parviflorus* Pourr. and *Salvia rosmarinus* Schleid. (formerly *Rosmarinus officinalis* L.). The oak tree functional type was inspired in *Quercus robur* L. which can also adopt a multi-stemmed shrub form after fire and coppicing, yet it recovers a tree form with time through self-thinning (Tavsanoğlu and Pausas 2018; Paula and others 2009). The model included additional information concerning the age of the plant cell when occupied and the number of seeds produced per cell, which corresponded to realistic values from literature (Figure 1; Table 1). The time steps used were of one year (that is $dt=1$ y). The simulations were performed by implementing a MATLAB R2015b code.

Soil Seedbank

We kept track of the soil seedbank SB_i at the plot scale (that is, the whole lattice), for each plant functional type i , by computing both the production and the seed input from neighbouring areas. We assumed that the seeds were dispersed homogeneously across the plot; thus, we multiplied each cell seed production rate, $SP_i(x)$, by the number of

cells that were occupied by mature individuals in the whole lattice. For pines and shrubs, the average numbers of seeds per cell, $N_{seeds_{1,2}}(x)$, were then calculated as the number of seeds in the soil seedbank, $SB_{1,2}$, divided by the total number of cells. In the case of oak tree, given the small number of seeds compared to the other species, the seeds locally produced and those arrived from elsewhere were randomly distributed across the cells in the lattice to calculate N_{seeds_3} . In the following, we detail how we implemented seed production and storage in the seed bank.

Seed Production

The annual pine seed production per cell $SP_1(x)$ was estimated at 100 seeds, which was calculated by considering that 10% of the average produced seeds would be available for germination after predation and seed loss (Vega and others 2008). Pine age of maturity (AM, the age at which a tree starts, on average, producing seeds) was defined as 10 years, as an approximation of the values reported for *Pinus pinaster* (Tapias and others 2001; Thanos and Daskalaku 2000).

The shrub species (either obligate seeder or facultative species) produced 1000 available seeds per occupied cell. It was considered that both the obligate seeder and the facultative shrub species started producing seeds after 2 years.

Finally, we defined that each mature oak tree produced 10 acorns per year that were available for germination (considering predation as well as seed and seedling loss, Gómez and others 2003). The oak trees reached maturity at 20 years [average value between field observation by Pausas (1999a) and the authors, unpublished].

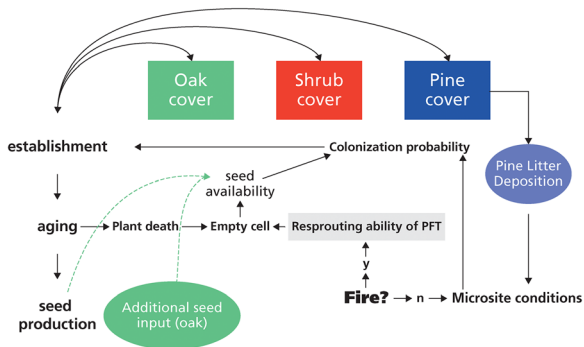


Figure 1. Schematic representation of the model indicating the variables involved in the development of pine, shrub and oak tree cover. The colonization of an empty cell depends on the colonization potential of each species (seed availability and seed production). The microsite conditions (represented by the influence of pine litter in a pine stand) will only influence colonisation when fire does not occur. In the case of oak, there is an additional seed input by birds from outside of the plot. In each model iteration, there is a test for the colonization of an empty cell, which will happen after a fire occurrence, depending on the model conditions. The resprouting ability of the plant functional type (PFT) was a key aspect of the model in determining the colonisation of an empty cell following fire.

Seed Bank

Depending on their specific strategy, each plant functional type was linked to different rules for the yearly seed bank update. Pines had a seed bank (serotinous cones) accumulating in the canopy over time (Vega and others 2008). We considered a degree of serotiny of 50%, which means that half of the seeds that were contained in serotinous cones before the fire were released after the fire (Table 1). Thus, every year, half of the seeds that were produced in each cell, $SP_1(x)$, were accumulated in the pine canopy bank (CB_1) and the other half was released to the soil: $SP_1(x) = DS * CB_1(x)$. The pine seeds remained viable in the soil for two years at most (De las Heras and others 2012): we simulated that 50% of the seeds died after the first year and the other 50% after the second year. In the case of the seeds of shrub species, the annual decay rate was set at 10%. Finally, the oak tree seed bank was re-set to zero yearly, due to the typical loss of viability during the first year of the seed (Hendry and others 1992).

Litter Accumulation

The accumulation of litter was a spatially explicit process that took place in the cells occupied by a mature pine tree as well as in their surrounding

eight cells (Moore neighbourhood). The litter content increased with an annual litter accumulation rate (Table 1), which was reduced to 20% of its value if the pines were not yet mature. The value obtained was the litter accumulation rate in the cell that was occupied by a pine tree, while the eight neighbours of this cell received 50% of this value. In the model, each year, part of the litter was degraded (40%), so that for a monospecific plantation of pine, a maximum litter depth (6 cm) was reached 20–30 years after pine plantation. All the litter values were based on field observations by experts.

Transition Rules: Plant Colonization and Mortality

The colonization of an empty cell was defined as a stochastic process that depended on the probability of establishment, $ProbC$, defined as: $ProbC_i = ProbS_i * ProbL_i$ for each species i ($i=1-3$). $ProbS_i$ depended on the number of available seeds and establishment capacity of species i and $ProbL_i$ depended on the microsite conditions, as represented by litter depth.

Given the fact that the habitat conditions were equally suitable for all three species, the probability of establishment $ProbS_i(x)$ of species i in a cell x was defined as a function of the seed number in the cell, $Nseeds_i(x)$, following Cannas and others (2003):

$$ProbS(x) = 1 - \left(1 - \frac{1}{E_i}\right)^{Nseeds_i(x)}$$

E_i represented the number of seeds that under optimal conditions would guarantee the dominance of the species i in a cell. The values of E_i for the different species represented a competition factor for the seedlings, which considering the differences in seed size between species, was approximated to differ by a factor of 10 between the different species. This number was set to 2 for the oak trees, 10 for the pines, 100 for the shrubs ($i=2, 10, 100$). For the oak tree, this value was established at 2 rather than 1, because the latter would lead to an establishment probability of almost 100%. The relations between the number of available seeds in a cell and the $ProbS_i$ for each species are shown in Figure 2.

Given the starting point of the system represented a pine plantation, the probability of establishment $ProbL_i$ in an empty cell was expressed as a function of litter depth, as we assumed that the increasing litter thickness over time would favour the relative dominance of the late successional species and, at the same time, inhibit the colonization of the early successional species (Figure 3; please see the equations in the appendix). More

specifically, the effect of litter thickness was defined as depending on seed size and thus on species regeneration strategy and successional stage. These assumptions were based on the following arguments: (i) bigger seeds typically do not present dormancy, whereas smaller seeds do and the breaking of this dormancy require fluctuations in temperature that do not occur when the litter layer is thicker than 1 cm; (ii) bigger seeds have higher elongation potential than smaller seeds and, thus, can establish themselves successfully under greater litter depths and (iii) bigger seeds are more susceptible to predation and/or desiccation than smaller seeds and, therefore, can benefit more from the protective effect of litter (both by hiding the seeds and by buffering climatic extremes). The values of the contribution due to litter depth to probability of establishment $ProbL_i(x)$ for the three different functional types were based on the literature (for example, Molofsky and Augspurger 1992; López-Barrera and González-Espinosa 2001; Fagúndez and Izco 2004; Kostel-Hughes and others 2005; Fernandes and Rigolot 2007; Giertych and Suszka 2011; Egawa and Tsuyuzaki 2013). Seed sizes for the different functional types were estimated as follows: the obligate seeder (for example, *Cistus* spp.) and facultative (for example, *Erica australis* L.) shrub species have small seeds (< 0.50 mg per seed, Thanos and others 1992; Fagúndez and Izco 2004; Vasques and others 2012); the pine tree (for example, *Pinus pinaster*) had intermediate size seeds (~54 mg per seed, García-Fayos 2001); the obligate resprouter tree (for example, *Quercus robur*) had large seeds (2–6 g per seed, García-Fayos 2001;

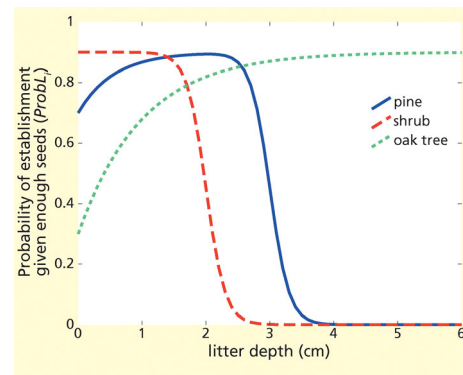


Figure 3. Probability of establishment in an empty cell given enough seeds are available ($ProbL$) to have maximum probability of establishment ($ProbS$), as a function of litter depth (cm) for pine (blue continuous line), shrub (red, dashed line) and oak tree (green dotted line).

Giertych and Suszka 2011). This information was complemented by author observations of the elongation potential of the different seeds during the cotyledon phase during germination experiments. See Figure 3 for the relations between litter depth and $ProbLi(x)$ for each functional type.

To decide which species will colonize a certain empty cell, we followed a standard approach to assign species to cells in proportion to the respective establishment probability. The species colonization probabilities in each cell were compared to a random number (r) drawn from a uniform distribution between 0 and 3. If the random number was smaller than the probability of colonization of species 1 ($r < ProbC_1$), the cell was colonized by species 1. Otherwise, if the number was smaller

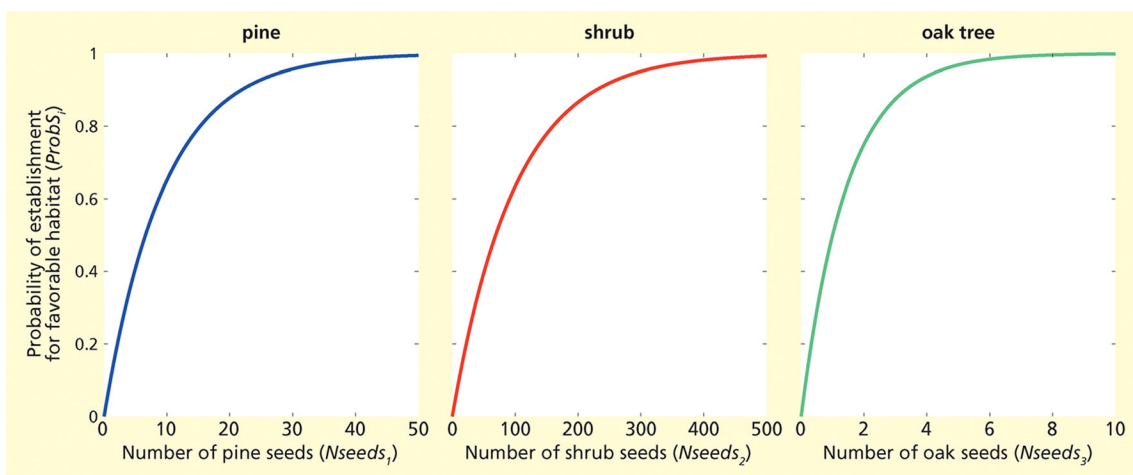


Figure 2. Probability of establishment ($ProbS$) for favourable environmental conditions in an empty cell, as a function of the number of available seeds for pine, shrub and oak tree. Notice the different scale for the x-axis, representing the number of seeds available per species. Differences are based in literature and result from differences in seed size and germination behaviour amongst species.

than the sum of the probabilities of species 1 and 2 ($ProbC_1 \leq r < ProbC_1 + ProbC_2$), species 2 colonized the cell. Species 3 colonized if $ProbC_1 + ProbC_2 \leq r < ProbC_1 + ProbC_2 + ProbC_3$, and otherwise the cell remained empty.

The annual mortality rate (*AMOrate*) of each species was defined as one over its life span (Baudena and others 2020).

Fire

Fire disturbance regime was defined stochastically, with the occurrence of fires expressed by an exponential distribution of return times (Kampen 1992; Baudena and others 2010). To study the response of the system to different fire frequency conditions, we selected three different average fire return times: seven, fifteen and thirty years, plus a scenario without fire. When a fire occurred, the species with resprouting ability (oak tree or facultative shrub species) continued to occupy the same cell, whereas pines and obligate seeder shrubs die. The fire that was simulated was of high severity, for which all the needles (crown) and litter (forest floor) were consumed, and seeder species killed. For the modelled forest type, with pine and shrubby understorey, wildfires naturally tend to be of high severity, primarily due to the cover, structural complexity and continuity of canopy and understorey fuels (García-Llamas and others 2019).

Model Simulation Settings

The initial conditions of the model were those of a pine plantation that developed for 100 years without fires, until it reached a mature stage. It was assumed that the system was not managed after the initial pine plantation. This simulated extensive pine plantations on old fields and degraded land with low presence of oak trees. In all cases, the model was run for 3000 years, with fires occurring after the initial 100 y. For each fire recurrence regime, ten different fire series were used in the model experiments and each set of conditions was repeated 20 times to account for the stochasticity of the model.

The model was initialized with a range of different initial conditions (for example, variable initial pine density, number of shrub seeds and variable annual acorn input; not shown). After learning that the model was mostly sensitive to the variation in yearly acorn input, the initial conditions for the model runs were then selected as follows: initial pine plantation interval: 4 cells between pines; 100 shrub seeds per cell (produced on site during the early development of the pine

plantation), number of oak seeds (acorns) across the plot given by the annual input, which, to obtain a broad spectrum, was simulated at 1, 5, 50 and 200 seeds.

The differences in the time at which oak trees reached relative dominance (more than 50% of cover of the cells in the lattice) in the communities with either obligate seeder or facultative shrub species were recorded. This was done separately for each combination of fire frequency, fire severity and values of yearly acorn input.

Statistical Analysis

The effect of fire frequency, regeneration types of shrub and number of oak seeds annual input on the time of 50% oak dominance (TOD 50) were tested using the nonparametric Kruskal–Wallis (KW) test for group comparisons. A three-way ANOVA could not be performed because the assumption of homoscedasticity was not met (significant Levene’s test at $F: 84.296; p < 0.001$). The Wilcoxon-test was used for pair-wise comparisons to test differences between groups for those variables that had a significant KW test and more than 2 groups for comparison (which was the case for the variable “number of oak seeds annual input”). The software R 4.1.2 was used to perform the statistical analysis.

RESULTS

In the absence of fire, the system attained a stochastically stable coexistence of the three plant types at steady state. This equilibrium was reached after about 500–1000 years from the initial pine plantation state and included predominantly oak trees (~75%) with co-existing pines (~20%) and both shrub types (< 5%) (Figure 4A, B).

The shifts in the relative dominance of each plant functional type over time relate to the respective lifespan: during the first decades the short lived, early successional shrub species dominated (about ~100 years at most after plantation), then the intermediate lived species (pine) dominated, and finally the long lived, late-successional species (oak tree) dominated (at ~250 years). The increase of the oak tree population was slow, but steady. In the absence of fire, neither the time when the equilibrium occurs nor the species that is dominant at the equilibrium (oak tree) were sensitive to changes in the values of the initial conditions.

The relative dominance of oak trees at steady state (that is, cover values higher than 50%, TOD 50) was maintained under all recurrence intervals

of high-severity fires (Figure 4C–F). The coexistence of all three functional types, however, was not observed when fires were simulated, since pines went extinct in all fire regimes, because of a combination of seed bank depletion and a reduction in empty sites available for pine establishment. Under high fire frequency conditions, obligate

seeder species were also eradicated from the system (average fire return time of 7 years; Figure 4H). Nevertheless, when the facultative shrub species was included in the simulations, a long-term coexistence of shrub and oak trees was reached under all fire disturbance regimes (Figure 4C, E, G). We found that there were no significant differences in

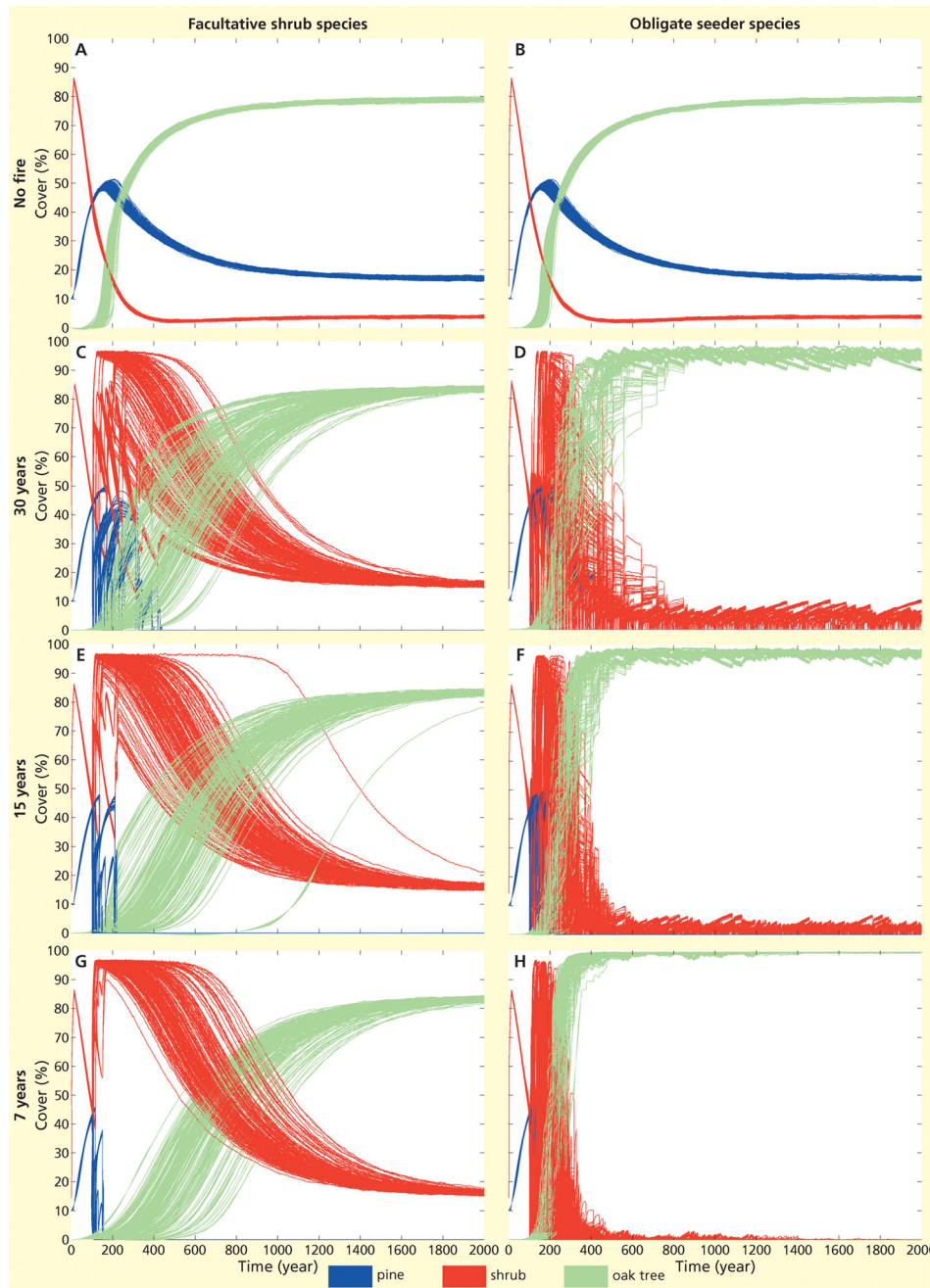


Figure 4. Plant species relative abundance (cover %) as a function of time for different return times of high-severity fires (from top to bottom: no fire, 30, 15 and 7 years) in communities with a facultative shrub species (left) or obligate seeder shrub (right). The lines correspond to 10 different stochastic fire series, with annual acorn input of 5 seeds per hectare, each repeated in 20 runs.

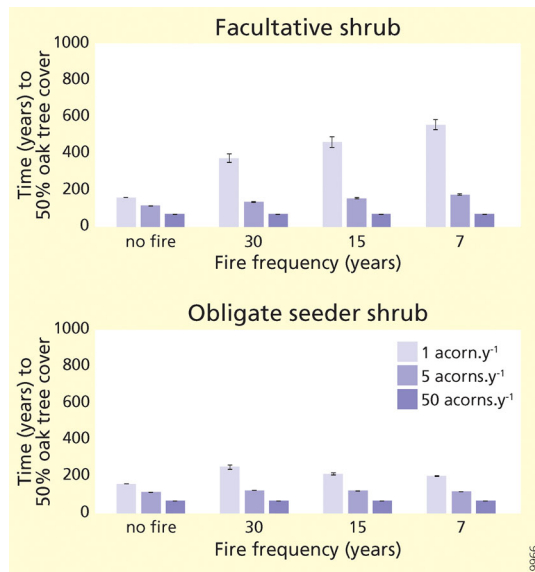


Figure 5. Average time and standard error (years) at which oak reached the cover of at least 50% for different fire interval averages (no fire, 30, 15 and 7 years) in communities with the functional types of facultative shrub or obligate shrub seeder, respectively, for conditions of different numbers of yearly input of oak acorns (1, 5 and 50).

TOD 50 in terms of the different fire frequencies (7, 15 and 30 years) considered (chi-squared=2.6139, df=2, p -value=0.2706). We did find, however, significant differences between the two regeneration types (obligate seeder and facultative species, chi-squared=39.69, df=1, p -value < 0.001) as well as between different amounts of yearly acorn input (Chi-squared=2804.4, df=2, p -value < 0.001). For the latter, significant differences were found between all the three different seed input values that were tested (1, 5 and 50 seeds per year following the Wilcoxon rank sum test for group comparisons, significance at $p < 0.001$).

The time at which pine trees were eradicated from the system depended exclusively on the fire return time (Figure 4C, E, G). Pine cover was eradicated (0% of cover) fastest at the highest fire frequency, namely we observe eradication times of about 40, 130 and 265 years, for fire frequency of 7, 15 and 30 years, respectively. These values did not change for different values of oak trees seed input or regeneration strategy of the shrub. However, the time at which oak trees reached dominance was not only dependent on fire frequency, but also on the resprouting capacity of the shrub (Figure 4C–H). In particular, high fire frequency accelerated oak tree dominance when the shrub was an obligate seeder but delayed it when the shrub had

resprouting ability (facultative shrub species; Figure 4C–H). This result was observed for all the input rates of oak tree seeds. However, oak tree dominance was delayed substantially (up to 550 years) when acorn input rates were very low (1 seed.year⁻¹, Figure 5).

Thus, the time at which oak trees reached dominance was shorter in communities with the obligate shrub species than in those with the facultative shrub species for all the three fire frequency regimes, whereas no difference was observed in the absence of fire (as expected).

DISCUSSION

We evaluated the role of plant characteristics, namely post-fire regeneration strategies of fire prone shrubs in influencing successional processes. Our model results indicated that the period of dominance of shrubs after fire is mostly dependent on their post-fire resprouting capacity, with a delay in succession caused by the resprouting capacity of the shrubs. This was due to spatial competition between species since a cell that is occupied by a facultative resprouter shrub remained occupied after a fire, while a cell that was occupied by an obligate seeder was empty after a fire. Field studies also suggested that the post-fire recovery of oak forests could be slow, with shrubland communities dominating in the first decades (Baeza and others 2007; Alvarez and others 2009). In short, we found that the facultative strategy (which regenerates both by seeds and resprouting) could delay succession for a considerable amount of time, in the order of centuries. This would likely lead to notable degradation, with increased erosion risk, reduced biodiversity, soil fertility, and potential for C sequestration (Mayor and others 2016; Van del Elsen and others 2020) and could be enhanced by climate change and aridity (Batllori and others 2017, 2019). In this context, the increase in the time of dominance of facultative shrub species that was observed in our model, highlights the importance of assessing the resprouter capacity of Mediterranean shrubs in response to recurrent fires.

In the absence of fire, our results showed a stable coexistence between shrubs, pines and oak trees. The time of species relative dominance related to their life span, in the sense that short lived species dominated earlier in the succession, whereas long lived species dominate later on, in agreement with the theory of initial floristic model of succession (Egler 1954). The relative dominance of late successional oak tree, such as *Quercus robur*,

in the Iberian Peninsula during the last ten thousand years was confirmed by paleobotanical records (Alcalde and others 2006). These records also suggested a long presence of *Pinus pinaster* in the Iberian Peninsula, prior to their widespread plantation by humans. Furthermore, sporadic fires might be favourable to pine communities, by creating open areas for pine colonization (López-Sáez and others 2010). Thus, the prevailing vegetation before intensive human impacts in the landscape probably consisted of a mixed pine-oak woodland and not of the typical climax vegetation suggested by the phytosociological model of Rivas-Martínez (1987), in which the tree layer was exclusively composed of oak species (Alcalde and others 2006; López-Sáez and others 2010). As expected, in the absence of fire, no differences between different shrub strategies were found since for modelling purposes only differences in post-fire regeneration strategy were considered. Previous model studies confirmed that in the absence of fire, the vegetation was dominated by early successional species, mainly *Pinus* spp. and with the passage of time this vegetation became dominated by later successional tree species (*Quercus* spp.). However, when early successional communities were affected by recurrent fires, plant succession can be arrested or delayed through a positive flammability-fire feedback loop, hence hampering fire resilience (Baudena and others 2020). A single fire is sometimes enough to change *Pinus* spp. forests into alternative stable states dominated by shrub communities. This trajectory deviation is more likely under high fire frequency regimes where the vegetation changes to dwarf shrubs and herbs (Santana and others 2010, 2014). In this line, post-fire recovery is expected to be faster in communities that are already dominated by oak trees before the fire than in communities that are dominated by pine or shrubs (Calvo and others 2003).

In our model, we observed the eradication of pines as a result of high frequency of severe fire. In fact, pine was eradicated at relatively low fire frequencies (30 years average fire return) as a result of some fire events occurring within 10 years after each other, because of the stochastic fire return time. This was caused by a combination of the depletion in the pine seed bank and by a reduction of empty sites available for post-fire pine establishment (competition). We expected that the eradication of pines would only occur at fire recurrence intervals shorter than the age of maturity of the pines, that is, 10 years; however, the stochastic variations in fire return time that were simulated in the model (with a possibility for

events of short fire recurrence intervals than the average frequency that is observed) can also be observed in nature.

According to our model results, oak trees also reached dominance under high fire frequency. In particular, oak trees were dominant at equilibrium in all the scenarios of fire disturbance, and this final outcome was not sensitive to changes in other model parameters, such as low acorn availability. These results agree with previous works (Baudena and others 2020) that found oak tree dominance in the long-term independently of the regime of fire occurrence. This pattern can be explained by the very high resprouting ability and long-life span of oak trees. Conversely, the other species tend to lose dominance over time, either because of having a short life span (shrubs) or a regeneration strategy that depends on local seed banks (pine and obligate seeder shrubs). Our results also agree well with the initial floristic model of succession (Egler 1954), according to which post-fire conditions tend to attain a similar state of equilibrium than the one that would be achieved in the absence of fire (Trabaud 1987). Furthermore, previous field studies suggested that oak tree species generally resprout rapidly and vigorously after fire under a wide set of conditions (Espelta and others 2003; Pausas 1997). Similar results were found under a frequent fire regime (Lloret and others 2003; Konstantinidis and others 2005), even after a period as short as three years after the last fire (Delitti and others 2005). These studies concerned forests that were already dominated by oak tree species, so that colonisation by oak tree species was not a limiting factor. In many instances, however, oak tree seed sources are distant, and there are few oak stands in the region, leading to very low acorn inputs from the surrounding areas, hence absolutely delaying the post-fire succession of pine forests (Acácio and others 2010; Urbietta and others 2011). Unfavourable environmental conditions for the regeneration of oak tree species, such as steep slopes and cold or dry sites, have been previously linked to the persistence of pine populations; however, such conditions were not simulated in our model (López-Sáez and others 2010). We have found that oak tree dominance under optimal conditions for oak establishment was accelerated by a higher yearly input of acorns, as expected. Previous research, however, has shown that the relative abundance of oak tree species depends strongly on their colonization potential and on the establishment success of oak seedlings (Sheffer 2012). Our model showed that a very small initial oak tree population and a small but steady yearly supply of 1 or 2 acorns per

hectare could lead to oak tree dominance within 200 years, at least in the absence of fire. This outcome was altered by frequent fire regimes, which led to a delay in oak tree dominance of a few centuries in cases of very low acorn supply (1 acorn per hectare per year). At yearly acorn supply values of 50 per hectare, frequent fire regimes no longer delayed oak tree dominance. In the field, acorn inputs strongly depend on the distance from seed sources, for example, on the presence and distribution of mature oak trees in the landscape. Because a low seed input has shown to influence the speed of oak tree dominance, we can expect that, understanding and manipulating the potential and effective dispersal of oak trees to the area can increase the presence of oak trees in the landscape. To do this, the promotion of acorn dispersers, such as the jay (*Garrulus glandarius* L.), could be considered (Ouden and others 2005). In this context, it is important to note that the type of plant community species dominance can interact with the colonization capacity of oak trees, as pine stands foster seed arrival, whereas shrublands are usually avoided by the jay because open areas usually lead to a higher exposure to predators (Pons and Pausas 2006). These mechanisms could inhibit oak tree colonization in highly dense shrublands, which could, in turn, lock the system in an early successional phase, especially when pines are eradicated from the system. This would agree well with the findings of Acácio and others (2007) who found seed arrival to be one of the limitations of oak tree establishment in shrublands.

Another factor that can lead to a decrease in oak tree numbers after a fire is resprouting failure, due to factors such as environmental stress, drought or age (Pausas 1999b; Baudena and others 2020). Pratt and others (2014) found a high mortality of facultative shrub species as a result of the combined action of frequent fires and post-fire drought. Furthermore, it is expected that resprouter species will have lower resprouting capacity and high mortality in dry areas (Ojeda and others 2005; Pausas and others 2015), which could undermine their dominance. If other factors such as drought were to be analysed, oak tree species might experience a greater reduction in abundance under likely climate change scenarios than pine or shrub species (Torres and others 2016; Batllori and others 2015, 2019; Baudena and others 2020), promoting shifts in species dominance as a result of high fire frequency. To further understand the effects of climate change scenarios on vegetation dynamics, research on the impacts of likely future climate conditions in oak tree establishment success as well

as in resprouting capacity of the shrubs is needed (Enright and others 2015).

The model presented here assumed resprouting behaviour of the main shrub species and the oak trees as a binomial feature, that is, a species either does or does not resprout after fire. However, it is presently known that post-fire resprouting capacity is actually a continuum, in terms of both the individual and the community response to a disturbance (for example, fire or herbivory) (Moreira and others 2011). In spite of the high relative abundance of resprouting species in several ecosystems around the globe and on their tendency to become numerous in less productive sites, a focus on the role of resprouters in community dynamics has been underrepresented in previous modelling and successional studies (Midgley 1996; Bond and Midgley 2001).

The plantation of extensive areas with pines in the Iberian Peninsula did not only target wood production interests, but also aimed to foster ecological succession, with pines as a pioneer species promoting the subsequent colonization by more resource-demanding late successional species (Zavala and others 2000). However, several studies have shown that, pine stands have largely failed to harbour late successional species, possibly because of their high planting densities (Maestre and Cortina 2004; Gavinet and others 2015). In this context, the use of mixed pine plantations including late successional species has been proposed to increase the resilience of pine forests to frequent wildfires as well as to foster and accelerate succession (Pausas and others 2004a, b; Vallejo and others 2009; Santana and others 2018). Our model results suggest that the composition of the understorey of pine stands should be considered, in particular regarding the resprouting capacity of fire-prone shrubs, as it can play an important role in constraining successional processes after pine has been eradicated from the system. Further research on the post-fire competitive effect of other facultative species with invasive behaviour in Portugal, such as acacia (*Acacia* spp.) and *Hakea sericea* Schrader, is needed since, according to our results, their potential to delay the establishment of oak tree populations could be enhanced by their regeneration strategy.

CONCLUSION

Our model indicated that the final succession state of pine-oak tree-shrub ecosystems is not influenced by fire frequency. The steady state dominated by oak trees is nearly insensitive to differences in ini-

tial model conditions. However, the time until oak tree dominance was reached was strongly delayed by the post-fire resprouting ability of understory shrub species. Our results showed the importance of considering the resprouting ability of understory shrubs in the assessment and management of pine forests that are subject to frequent fires, as a high post-fire resprouting capacity could inhibit plant succession for several centuries, especially under low levels of acorn yearly input, which could, in turn, lead to extensive post-fire erosion and degradation.

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DATA AVAILABILITY

Data can be accessed at <https://doi.org/10.25397/eur.19131320>.

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