Ecosystems (2023) 26: 146–160
https://doi.org/10.1007/s10021-022-00750-z

ECOSYSTEMS

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

A. Vasques,[1,2,3]* M. Baudena,[2,4] V. R. Vallejo,[5] S. Kéfi,[6] S. Bautista,[7]
V. M. Santana,[3,8] M. J. Baeza,[7] P. Maia,[3] J. J. Keizer,[3] and M. Rietkerk[2]

Erasmus University College, Erasmus University Rotterdam, Nieuwemarkt 1A, 3011HP Rotterdam, The Netherlands; Copernicus Institute of Sustainable Development, Environmental Sciences Group, Utrecht University, 3508 TC Utrecht, The Netherlands; Centre for Environmental and Marine Studies (CESAM). Department of Environment and Planning, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal; National Research Council of Italy, Institute of Atmospheric Sciences and Climate (CNR-ISAC), Corso Fiume 4, 10133 Torino, Italy; Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, Av. Diagonal, 643, 08028 Barcelona, Spain; CNRS, IRD, EPHE, Institut Des Sciences de L'Evolution, Université de Montpellier, CC 065, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France; Department of Ecology and IMEM, University of Alicante, Campus de San Vicente del Raspeig, 03690 Alicante, Spain; Mediterranean Center for Environmental Studies (CEAM), Parque Tecnológico C/Charles R. Darwin, 14, 46980 Paterna, Spain

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 understory 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

---

Received 28 July 2021; accepted 5 February 2022;

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-022-00750-z.

Author contributions: A. Vasques contributed to model development, expert knowledge, code development, data analysis, writing the paper. M. Baudena contributed to model development, code development, writing the paper. R. Vallejo contributed to model development, expert knowledge on plant successional dynamics, fire frequency, severity and restoration and writing the paper. S. Kéfi contributed to model development, reviewing the paper. S. Bautista contributed to expert knowledge in Mediterranean post-fire successional dynamics, writing the paper. V.M. Santana contributed to expert knowledge in Mediterranean post-fire successional dynamics, writing the paper. J. Baeza contributed to expert knowledge in Mediterranean post-fire successional dynamics, writing the paper. P. Maia contributed to expert knowledge on fire severity and species regeneration strategies, reviewing the paper. J.J. Keizer contributed to model development, expert knowledge on post-fire succession in Portugal and writing the paper. M. Rietkerk contributed to model development and writing the paper.

*Corresponding author; e-mail: vasques@euc.eur.nl

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 simulation 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 (Keeley 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 understory 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}	*a*
DS	Degree of serotiny	0.5	–	–	–	*a*
lrate	Annual litter accumulation rate	0.8			cm y^{-1}	
AM	Age of maturity	10	2	20	y	*b*
E_i	Competition factor for the seedlings	10	100	2		–
AMOrate	Annual mortality rate	1/100	1/30	1/1000	y	*c*

---

[a] *Gómez and others (2003) and Vega and others (2008).*

[b] *For Pinus spp.: Tapias and others (2001); Thanos and Daskalakou (2000); for oak: Pausas (1999a) and the authors, unpublished.*

[c] *Baudena 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 (Tavsanoglu 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, $\mathrm{Nseeds}_{1,2}(x)$, 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 Nseeds_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 Daskalakou 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].

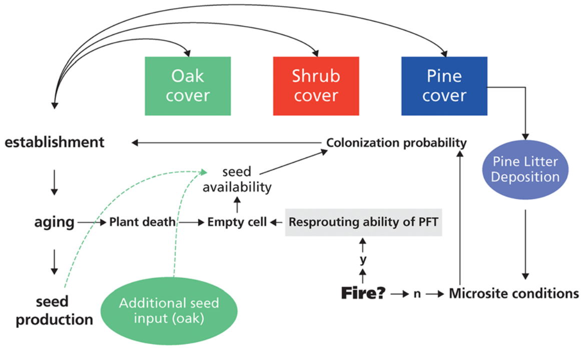

Figure 1. Schematic representation of the model indicating the variables involved in the development of pine, shrub and oak tree cover. The colonization of an empty cell depends on the colonization potential of each species (seed availability and seed production). The microsite conditions (represented 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, $\mathrm{SP}_1(x)$, were accumulated in the pine canopy bank (CB_1) and the other half was released to the soil:$SP_1(x) = \mathrm{DS}*CB_1(x)$. 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; 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.

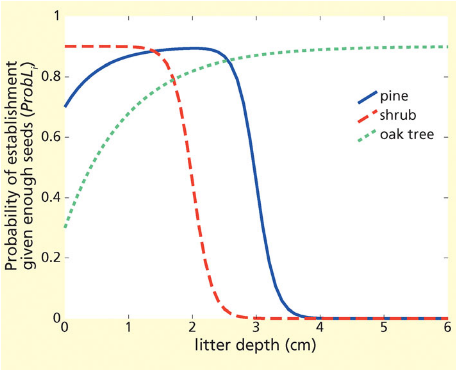

Figure 3. Probability of establishment in an empty cell given enough seeds are available (Prob*L*) to have maximum probability of establishment (Prob*S*), as a function of litter depth (cm) for pine (blue continuous line), shrub (red, dashed line) and oak tree (green dotted line).

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

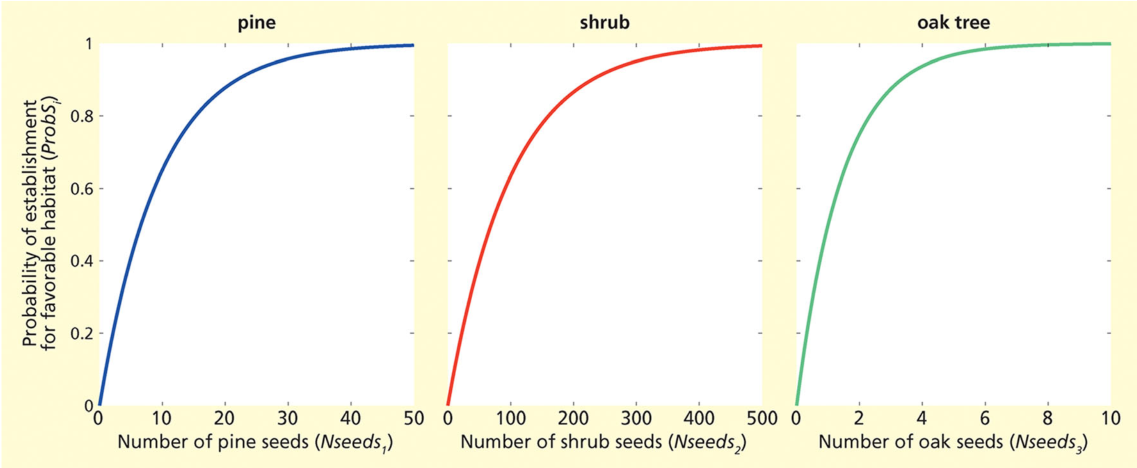

Figure 2. Probability of establishment (*ProbS*) for favourable environmental conditions in an empty cell, as a function of the number of available seeds for pine, shrub and oak tree. Notice the different scale for the x-axis, representing the number of seeds available per species. Differences are based 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 understory, wildfires naturally tend to be of high severity, primarily due to the cover, structural complexity and continuity of canopy and understory 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

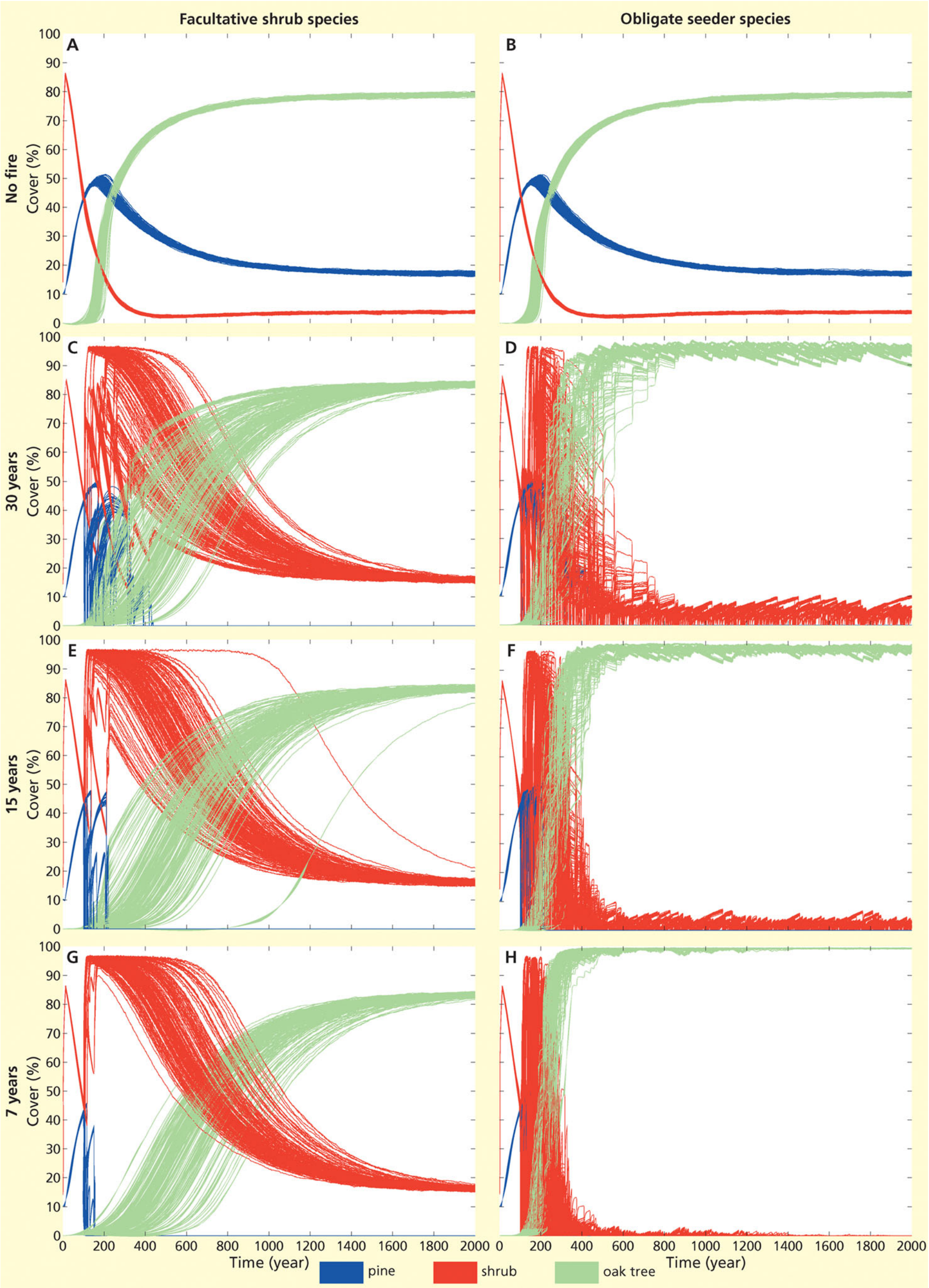

Figure 4. Plant species relative abundance (cover %) as a function of time for different return times of high-severity fires (from top to bottom: no fire, 30, 15 and 7 years) in communities with a facultative shrub species (left) or obligate seeder shrub (right). The lines correspond to 10 different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

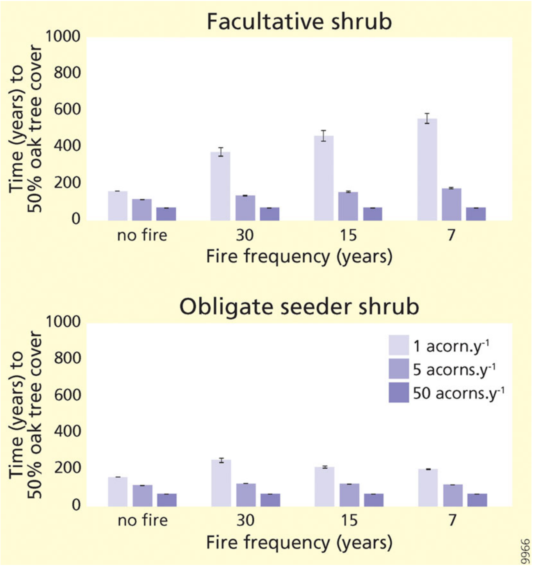

Figure 5. Average time and standard error (years) at which oak reached the cover of at least 50% for different fire interval averages (no fire, 30, 15 and 7 years) in communities with the functional types of facultative shrub or obligate shrub seeder, respectively, for conditions of different numbers 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; Urbieta 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 understory 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 initial model conditions. However, the time until oak tree dominance was reached was strongly delayed by the post-fire resprouting ability of understorey shrub species. Our results showed the importance of considering the resprouting ability of understorey 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.

ACKNOWLEDGEMENTS

We would like to thank Oscar Gonzalez-Pelayo, Angeles García-Mayor, Peter de Ruiter and Florian D. Schneider for their comments and suggestions. The authors are also grateful to Ton Markus for editing the final figures and to two anonymous reviewers as well as to the journal editors for their comments, which greatly contributed to improve the manuscript.

FUNDING

This research has received funding from the European Union Seventh Framework Programme (FP7/2007-2013) under the grant agreement no. 283068 (CASCADE project). Thanks are due to FCT/MCTES for the financial support to CESAM (UIDP/50017/2020+UIDB/50017/2020), through national funds and the post-doctoral research contract of Jacob Keizer (FCT-IF/01465/2015), and to the Spanish Ministry of Science and Innovation for financial support (CGL2017-89804-R) of the work of Susana Bautista. The work of Paula Maia was partially supported by the project SuSPiRe (PTDC/ASP-SIL/30983/2017) funded by FCT, through COMPETE2020—Programa Operacional Competitividade e Internacionalização (POCI).

OPEN ACCESS

DATA AVAILABILITY

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

REFERENCES

Acácio V, Holmgren M, Jansen PA, Schrotter O. 2007. Multiple recruitment limitation causes arrested succession in Mediterranean cork oak systems. Ecosystems 107:1220–1230.

Acácio V, Holmgren M, Rego F, Moreira F, Mohren GM. 2009. Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands? Agrofood Systems 762:389–400.

Acácio V, Holmgren M, Moreira F, Mohren GM. 2010. Oak persistence in Mediterranean landscapes: the combined role of management topography and wildfires. Ecology and Society 154:40.

Alcalde C, Amorena IG, Álvarez SG, Calvo DG, García RG, Génova M, Del Nido J. 2006. Contribución de la Paleofitogeografía a la interpretación del paisaje vegetal ibérico Investigación agraria Sistemas y recursos forestales. Forest Systems 151:40–54.

Alvarez R, Munoz A, Pesqueira XM, Garcia-Duro J, Reyes O, Casal M. 2009. Spatial and temporal patterns in structure and diversity of Mediterranean forest of *Quercus pyrenaica* in relation to fire. Forest Ecology and Managment 2577:1596–1602.

Baeza MJ, Valdecantos A, Alloza JA, Vallejo VR. 2007. Human disturbance and environmental factors as drivers of long-term post-fire regeneration patterns in Mediterranean forests. Journal of Vegetation Science 182:243–252.

Batllori E, Ackerly DD, Moritz MA. 2015. A minimal model of fire-vegetation feedbacks and disturbance stochasticity generates alternative stable states in grassland–shrubland–woodland systems. Environmental Research Letters 10:34018.

Batllori E, De Cáceres M, Brotons L, Ackerly DD, Moritz MA, Lloret F. 2017. Cumulative effects of fire and drought in Mediterranean ecosystems. Ecosphere 88:e01906.

Batllori E, De Caceres M, Brotons L, Ackerly DD, Moritz MA, Lloret F. 2019. Compound fire-drought regimes promote ecosystem transitions in Mediterranean ecosystems. Journal of Ecology 107:1187–1198.

Baudena M, D'Andrea F, Provenzale A. 2010. An idealized model for tree–grass coexistence in savannas: the role of life stage structure and fire disturbances. Journal of Ecology 981:74–80.

Baudena M, Santana VM, Baeza MJ, Bautista S, Eppinga MB, Hemerik L, Garcia Mayor A, Rodriguez F, Valdecantos A, Vallejo VR, Vasques A, Rietkerk M. 2020. Increased aridity drives post-fire recovery of Mediterranean forests towards open shrublands. New Phytologist 2254:1500–1515.

Bond WJ, Midgley JJ. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology & Evolution 16(1):45–51.

Calvo L, Santalla S, Marcos E, Valbuena L, Tárrega R, Luis E. 2003. Regeneration after wildfire in communities dominated by *Pinus pinaster* an obligate seeder and in others dominated by *Quercus pyrenaica* a typical resprouter. Forest Ecology and Managment 1841:209–223.

Cannas SA, Marco DE, Páez SA. 2003. Modelling biological invasions: species traits species interactions and habitat heterogeneity. Mathematical Biosciences 1831:93–110.

Cerabolini B, Ceriani RM, Caccianiga M, De Andreis R, Raimondi B. 2003. Seed size and shape and persistence in soil: a test on Italian flora from Alps to Mediterranean coasts. Seed Science Research 13:75–86.

Clements FE. 1916. Plant Succession: An Analysis of the Development of Vegetation Carnegie Institute of Washington Washington.

Connell JH, Slatyer RO. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111:1119–1144.

De las Heras J, Moya D, Vega JA, Daskalakou E, Vallejo VR, Grigoriadis N, Fernandes P. 2012. Post-Fire Management of Serotinous Pine Forests eds Moreira F, Arianoutsou M, Corona P, De Las Heras J. In Post-Fire Management and Restoration of Southern European Forests Springer Netherlands pp 121–150.

Delitti W, Ferran A, Trabaud L, Vallejo VR. 2005. Effects of fire frequency in *Quercus coccifera* L shrublands of the Valencia Region Spain: I plant composition and productivity. Plant Ecology 1771:57–70.

Díaz-Delgado R, Lloret F, Pons X, Terradas J. 2002. Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. Ecology 838:2293–2303.

Díaz-Delgado R, Lloret F, Pons X. 2003. Influence of fire severity on plant regeneration by means of remote sensing imagery. International Journal of Remote Sensing 248:1751–1763.

Durrett R, Levin SA. 1994. Stochastic spatial models: a user's guide to ecological applications. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 343 (1305):329–350.

Egler FE. 1954. Vegetation science concepts I Initial floristic composition a factor in old-field vegetation development with 2 figs. Vegetatio 4 412–417.

Egawa C, Tsuyuzaki S. 2013. The effects of litter accumulation through succession on seed bank formation for small and large seed species. Journal of Vegetation Science 246:1062–1073.

Enright NJ, Fontaine JB, Bowman DM, Bradstock RA, Williams RJ. 2015. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Frontiers in Ecology and the Environment 135:265–272.

Espelta JM, Retana J, Habrouk A. 2003. Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites. Forest Ecology and Management 1791:401–414.

Facelli JM, Pickett ST. 1991. Plant litter: its dynamics and effects on plant community structure. The Botanical Review 571:1–32.

Fagúndez J, Izco J. 2004. Seed morphology of *Calluna salisb* Ericaceae. Acta Botanica Malacitana 29:215–220.

Farrell C, Hobbs RJ, Colmer TD. 2012. Microsite and litter cover effects on seed banks vary with seed size and dispersal mechanisms: implications for revegetation of degraded saline land. Plant Ecology 2137:1145–1155.

Fernandes PM, Rigolot E. 2007. The fire ecology and management of maritime pine *Pinus pinaster* Ait. Forest Ecology and Managment 2411:1–13.

García-Fayos P. 2001. Bases ecológicas para la recolección almacenamiento y germinación de semillas de especies de uso forestal en la Comunidad Valenciana Book ID: 6170 Generalitat Valenciana Spain.

García-Llamas P, Suárez-Seoane S, Taboada A, Fernández-Manso A, Quintano C, Fernández-García V, Fernández-Guisuraga JM, Marcos E, Calvo L. 2019. Environmental drivers of fire severity in extreme fire events that affect Mediterranean pine forest ecosystems. Forest Ecology and Management 433:24–32.

Gaudio N, Balandier P, Dumas Y, Ginisty C. 2011. Growth and morphology of three forest understorey species *Calluna vulgaris Molinia caerulea and Pteridium aquilinum* according to light availability. Forest Ecology and Managment 2613:489–498.

Gavinet J, Vilagrosa A, Chirino E, Granados ME, Vallejo VR, Prévosto B. 2015. Hardwood seedling establishment below Aleppo pine depends on thinning intensity in two Mediterranean sites. Annals of Forest Science 728:999–1008.

Giertych MJ, Suszka J. 2011. Consequences of cutting off distal ends of cotyledons of *Quercus robur* acorns before sowing. Annals of Forest Science 682:433–442.

Gómez JM, Garcıa D, Zamora R. 2003. Impact of vertebrate acorn-and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. Forest Ecology and Managment 1801–3:125–134.

Hendry GA, Finch-Savage WE, Thorpe PC, Atherton NM, Buckland SM, Nilsson KA, Seel WE. 1992. Free radical processes and loss of seed viability during desiccation in the recalcitrant species *Quercus robur* L. New Phytologist 1222:273–279.

Kampen N. 1992. Stochastic processes in Physics and Chemistry Stochastic Processes in Physics and Chemistry Revised and enlarged edition Publisher: Elsevier Science Amsterdam.

Keeley JE. 1986. Resilience of Mediterranean shrub communities to fires In: Resilience in Mediterranean-Type Ecosystems eds D Bell A J M Hopkins & B B Lamont Dr W Junk Dordrecht p 95–112.

Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW. Eds. 2012. Fire in Mediterranean Ecosystems Ecology Evolution and Management Cambridge University Press New York NY USA.

Konstantinidis P, Tsiourlis G, Galatsidas S. 2005. Effects of wildfire season on the resprouting of kermes oak *Quercus coccifera* L. Forest Ecology and Managment 2081:15–27.

Kostel-Hughes F, Young TP, Wehr JD. 2005. Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation to seed size. The Journal of the Torrey Botanical Society 1321:50–61.

Lamont BB, Witkowski ETF, Enright NJ. 1993. Post-fire litter microsites: safe for seeds unsafe for seedlings. Ecology 74 (2):501–512.

Lloret F, Pausas JG, Vilà M. 2003. Responses of Mediterranean Plant Species to different fire frequencies in Garraf Natural Park Catalonia Spain: field observations and modelling predictions. Plant Ecology 1672:223–235.

López-Barrera F, González-Espinosa M. 2001. Influence of litter on emergence and early growth of *Quercus rugosa*: a laboratory study. New Forests 211:59–70.

López-Poma R, Orr BJ, Bautista S. 2014. Successional stage after land abandonment modulates fire severity and post-fire recovery in a Mediterranean mountain landscape. International Journal of Wildland Fire 237:1005–1015.

López-Sáez JA, López-Merino L, Alba-Sánchez F, Pérez-Díaz S, Abel-Schaad D, Carrión JS. 2010. Late Holocene ecological history of *Pinus pinaster* forests in the Sierra de Gredos of central Spain. Plant Ecology 2062:195–209.

Loydi A, Eckstein RL, Otte A, Donath TW. 2013. Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis. Journal of Ecology 1012:454–464.

Maestre FT, Cortina J. 2004. Are *Pinus halepensis* plantations useful as a restoration tool in semiarid Mediterranean areas? Forest Ecology and Managment 1981:303–317.

Maia P, Pausas JG, Vasques A, Keizer JJ. 2012. Fire severity as a key factor in post-fire regeneration of *Pinus pinaster* Ait in Central Portugal. Annals of Forest Science 694:489–498.

Mayor AG, Valdecantos A, Vallejo V, Keizer J, Bloem J, Baeza J, González-Pelayo O, Machado AI, de Ruiter PC. 2016. Fire-induced pine woodland to shrubland transitions in Southern Europe may promote shifts in soil fertility. Science of the Total Environment 573:1232–1241.

Midgley JJ. 1996. Why the world's vegetation is not totally dominated by resprouting plants; because resprouters are shorter than reseeders. Ecography 19:92–95.

Molofsky J, Augspurger CK. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73 (1):68–77.

Moreira F, Viedma O, Arianoutsou M, Curt T, Koutsias N, Rigolot E, Bilgili E. 2011. Landscape–wildfire interactions in southern Europe: implications for landscape management. Journal of Environmental Managment 9210:2389–2402.

Ojeda F, Brun FG, Vergara JJ. 2005. Fire rain and the selection of seeder and resprouter life-histories in fire-recruiting woody plants. New Phytologist 1681:155–165.

Ouden J, Jansen PA, Smit R. 2005. Jays Mice and Oaks: Predation and Dispersal of *Quercus robur* and *Q petraea* in North-western Europe in Lambert J E Hulme P E & Vander Wall S B eds Seed fate: predation dispersal and seedling establishment CABI p 223.

Paula S, Arianoutsou M, Kazanis D, Tavsanoglu Ç, Lloret F, Buhk C, Ojeda F, Luna B, Moreno JM, Rodrigo A, Espelta JM, Palacio S, Fernández-Santos B, Fernandes PM, Pausas JG. 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology 90:142.

Paula S, Pausas JG. 2008. Burning seeds: germinative response to heat treatments in relation to resprouting ability. Journal of Ecology 963:543–552.

Pausas JG. 1997. Resprouting of *Quercus suber* in NE Spain after fire. Journal of Vegetation Science 8:703–706. https://doi.org/10.2307/3237375.

Pausas JG. 1999a. Mediterranean vegetation dynamics: modelling problems and functional types. Plant Ecology 1401:27–39.

Pausas JG. 1999b. Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: A simulation approach. Journal of Vegetation Science 10:717–722. https://doi.org/10.2307/3237086.

Pausas JG, Bladé C, Valdecantos A, Seva JP, Fuentes D, Alloza JA, Vilagrosa A, Bautista S, Cortina J, Vallejo VR. 2004a. Pines and oaks in the restoration of Mediterranean landscapes of Spain: new perspectives for an old practice—a review. Plant Ecology 1711–2:209–220.

Pausas JG, Bradstock RA, Keith DA, Keeley JE, Fire GCTE, Network. 2004b. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85:1085–1100.

Pausas JG, Pratt RB, Keeley JE, Jacobsen AL, Ramirez AR, Vilagrosa A, Paula S, Kaneakua-Pia IN, Davis SD. 2015. Towards understanding resprouting at the global scale. New Phytologist 2093:945–954.

Pons J, Pausas JG. 2006. Oak regeneration in heterogeneous landscapes: the case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. Forest Ecology and Managment 2311:196–204.

Pons J, Pausas JG. 2007. Acorn dispersal estimated by radio-tracking. Oecologia 153:903–911.

Pratt RB, Jacobsen AL, Ramirez AR, Helms AM, Traugh CA, Tobin MF, Davis S. 2014. Mortality of resprouting chaparral shrubs after a fire and during a record water scarcity: 480 physiological mechanisms and demographic consequences. Global Change Biology 20:893–907.

Rodrigo A, Retana J, Picó X. 2004. Direct regeneration is not the only response of Mediterranean forests to large fires. Ecology 85:716–729.

Rivas-Martínez S. 1987. Mapa de Series de Vegetación de España Memoria del Mapa de Series de Vegetación de España ICONA Madrid.

Santana VM, Baeza MJ, Marrs RH, Vallejo VR. 2010. Old-field secondary succession in SE Spain: may fire divert it? Plant Ecology 211:337–349.

Santana VM, Alday JG, Baeza MJ. 2014. Effects of fire regime shift in Mediterranean Basin ecosystems: changes in soil seed bank composition among functional types. Plant Ecology 215:555–566.

Santana VM, Baeza MJ, Valdecantos A, Vallejo VR. 2018. Redirecting fire-prone Mediterranean ecosystems toward more resilient and less flammable communities. Journal of Environmental Management 215:108–115.

Sheffer E. 2012. A review of the development of Mediterranean pine–oak ecosystems after land abandonment and afforestation: are they novel ecosystems? Annals of Forest Science 694:429–443.

Tapias R, Gil L, Fuentes-Utrilla P, Pardos JA. 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. Journal of Ecology 894:629–638.

Thanos CA, Georghiou K, Kadis C, Pantazi C. 1992. Cistaceae: a plant family with hard seeds. Israel Journal of Botany 414–6:251–263.

Thompson K. 2000. The functional ecology of soil seed banks in Michael Fenner ed Seeds: the ecology of regeneration in plant communities CAB international pp: 215–235.

Torres I, Pérez B, Quesada J, Viedma O, Moreno JM. 2016. Forest shifts induced by fire and management legacies in a *Pinus pinaster* woodland. Forest Ecology and Managment 361:309–317.

Trabaud L. 1987. Natural and Prescribed Fire: Survival Strategies of Plants and Equilibrium in Mediterranean Ecosystems in Plant Response to Stress NATO ASI Series 15:607–621.

Tavsanoglu Ç, Pausas JG. 2018. A functional trait database for Mediterranean Basin plants. Scientific Data 5:180135.

Thanos CA, Daskalakou EN. 2000. Reproduction in *Pinus halepensis* and *P brutia* In: Ne´eman G, Trabaud L eds. Ecology biogeography and management of *Pinus halepensis* and *P brutia* forest ecosystems in the Mediterranean Basin p 79–90 Backhuys Leiden NL.

Urbieta IR, García LV, Zavala MA, Marañón T. 2011. Mediterranean pine and oak distribution in southern Spain: Is there a mismatch between regeneration and adult distribution? Journal of Vegetation Science 221:18–31.

Vallejo VR, Serrasolses I, Alloza JA, Baeza MJ, Bladé C, Chirino E, Duguy B, Fuentes D, Pausas JG, Valdecantos A, Vilagrosa A. 2009. Long-term restoration strategies and techniques in Cerda A, Robichaud P eds. Fire Effects on Soils and Restoration Strategies Science Publishers Inc Enfield p 373–398.

Vallejo VR, Allen EB, Aronson J, Pausas JG, Cortina J, Gutiérrez JR. 2012a. Restoration of Mediterranean-type woodlands and shrublands in Van Andel J, Aronson J eds. Restoration ecology: the new frontier 2nd edn Wiley Chichester p 130–144.

Vallejo VR, Arianoutsou M, Moreira F. 2012b. Fire ecology and post-fire restoration approaches in Southern European forest types in Moreira F, Arianoutsou M, Corona P, De las Heras J eds. Post-Fire Management and Restoration of Southern European Forests. Springer Netherlands p 93–119.

Van den Elsen E, Stringer LC, De Ita C, Hessel R, Kéfi S, Schneider FD, Bautista S, Mayor Angeles G, Baudena M, Rietkerk M, Valdecantos A, Vallejo VR., Geeson N, Brandt CJ, Fleskens L, Hemerik L, Panagos P, Valente S, Keizer JJ, Schwilch G, Jucker RM, Sietz D, Christoforou M, Hadjimitsis DG, Papoutsa C, Quaranta G, Salvia R, Tsanis IK, Daliakopoulos I, Claringbould H, de Ruiter PC. 2020. Advances in understanding and managing catastrophic ecosystem shifts in Mediterranean ecosystems. Frontiers in Ecology and Evolution 8: 561101.

Vasques A, Maia P, Pedro M, Santos C, Vallejo VR, Keizer JJ. 2012. Germination in five shrub species of Maritime Pine understory - does seed provenance matter? Annals of Forest Science 694:499–507.

Vega JA, Fernández C, Pérez-Gorostiaga P, Fonturbel T. 2008. The influence of fire severity serotiny and post-fire management on *Pinus pinaster* Ait recruitment in three burnt areas in Galicia NW Spain. Forest Ecology and Managment 2569:1596–1603.

Wolfram S. 1984. Cellular Automata as Models of Complexity Nature 3115985:419–424.

Xiong S, Nilsson C. 1999. The effects of plant litter on vegetation: a meta-analysis. Journal of Ecology 876:984–994.

Zavala MA, Espelta JM, Retana J. 2000. Constraints and tradeoffs in Mediterranean plant communities: the case of holm oak-Aleppo pine forests. The Botanical Review 661:119–149.

Terms and Conditions

Springer Nature journal content, brought to you courtesy of Springer Nature Customer Service Center GmbH (“Springer Nature”).

Springer Nature supports a reasonable amount of sharing of research papers by authors, subscribers and authorised users (“Users”), for small-scale personal, non-commercial use provided that all copyright, trade and service marks and other proprietary notices are maintained. By accessing, sharing, receiving or otherwise using the Springer Nature journal content you agree to these terms of use (“Terms”). For these purposes, Springer Nature considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the relevant terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). For Creative Commons-licensed articles, the terms of the Creative Commons license used will apply.

We collect and use personal data to provide access to the Springer Nature journal content. We may also use these personal data internally within ResearchGate and Springer Nature and as agreed share it, in an anonymised way, for purposes of tracking, analysis and reporting. We will not otherwise disclose your personal data outside the ResearchGate or the Springer Nature group of companies unless we have your permission as detailed in the Privacy Policy.

While Users may use the Springer Nature journal content for small scale, personal non-commercial use, it is important to note that Users may not:

1. use such content for the purpose of providing other users with access on a regular or large scale basis or as a means to circumvent access control;
2. use such content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval , sponsorship, or association unless explicitly agreed to by Springer Nature in writing;
4. use bots or other automated methods to access the content or redirect messages
5. override any security feature or exclusionary protocol; or
6. share the content in order to create substitute for Springer Nature products or services or a systematic database of Springer Nature journal content.

In line with the restriction against commercial use, Springer Nature does not permit the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Springer Nature journal content cannot be used for inter-library loans and librarians may not upload Springer Nature journal content on a large scale into their, or any other, institutional repository.

These terms of use are reviewed regularly and may be amended at any time. Springer Nature is not obligated to publish any information or content on this website and may remove it or features or functionality at our sole discretion, at any time with or without notice. Springer Nature may revoke this licence to you at any time and remove access to any copies of the Springer Nature journal content which have been saved.

To the fullest extent permitted by law, Springer Nature makes no warranties, representations or guarantees to Users, either express or implied with respect to the Springer nature journal content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Springer Nature that may be licensed from third parties.

If you would like to use or distribute our Springer Nature journal content to a wider audience or on a regular basis or in any other manner not expressly permitted by these Terms, please contact Springer Nature at

onlineservice@springernature.com