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

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1 **Post-fire regeneration traits of understory shrub species modulate**  
2 **successional responses to high severity fire in Mediterranean pine forests**

3

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26

27 **Abstract**

28 Recurrent fires can impede the spontaneous recruitment capacity of pine forests.  
29 Empirical studies have suggested that this can lead to a prolonged replacement  
30 of pine forest by shrubland, especially if shrub species are pyrophytic. Model-  
31 based studies, however, have suggested that post-fire succession of pine forest  
32 under current climatic conditions will eventually tend towards the dominance of  
33 oaks, even under high fire recurrence. These previous modelling studies did not  
34 address the role of the various post-fire regeneration traits of the understory shrub  
35 species. Considering the dichotomy of obligate seeder vs. resprouter species,  
36 either obligate or facultative resprouter, we hypothesized that when the shrubs  
37 present are post-fire seeders, the oaks steadily occupy the forest, whereas  
38 resprouter shrub species might compete with oaks and delay or arrest post-fire  
39 succession.

40 To test this hypothesis, we developed a dynamic, cellular automaton model for  
41 simulating post-fire successional transitions in pine forests, including shrubs,  
42 pines and oaks, and stochastic fires of regular frequency.

43 Our results showed a strong tendency towards oak dominance as final model  
44 state and a very reduced role of fire recurrence in this final state, with low yearly  
45 acorn input delaying oak dominance. Most relevantly, and in line with our  
46 hypothesis, the trend towards oak dominance depended markedly on the two  
47 types of shrub species, being delayed by resprouter species, which extended the  
48 shrub-dominated succession stage for several centuries. Our simulation results  
49 supported the view that the type of understorey species should be a key  
50 consideration in post-fire restoration strategies aiming to enhance ecosystem  
51 resilience.

52 **Keywords**

- 53 ○ facultative shrub species
- 54 ○ obligate seeder shrub species
- 55 ○ pine forests
- 56 ○ arrested succession
- 57 ○ Mediterranean plant communities
- 58 ○ cellular automata
- 59 ○ wildfires
- 60 ○ oak regeneration

61 **Manuscript highlights**

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

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111 consideration in post-fire restoration strategies aiming to enhance fire resilience.

112

### 113 **Introduction**

114 In the past fifty years, Mediterranean landscapes experienced intense changes  
115 that led to abandonment of marginal croplands, on the one hand, and, on the  
116 other hand, to extensive afforestation with pine plantations (Pausas and others  
117 2004; Vallejo and others 2012 ab). These changes have contributed to  
118 intensifying fire regimes in the Mediterranean Basin, which in turn, can have  
119 pronounced effects on the composition and long-term resilience of its plant  
120 communities (Diaz-Delgado and others 2002; Vallejo and others 2012 ab).

121 According to the classical view on succession, species replacement in the  
122 absence of disturbance is driven by facilitation mechanisms, with early  
123 successional species creating conditions that are less favourable for themselves  
124 than for late successional species (Clements 1916; Connell and Slatyer 1977). In  
125 line with this theory, undisturbed Mediterranean pine forests are considered to  
126 foster successional processes, in particular by creating conditions under their  
127 canopy that are favourable for the establishment of late successional species  
128 (e.g. *Quercus ilex*; Zavala and others 2000). Most Mediterranean plant species  
129 are well adapted to fire occurrence, responding to fire through three main  
130 regeneration strategies (also called plant functional types, PFT): i) plant survival  
131 through the resistance of below-ground buds to fire, followed by resprouting of  
132 the above-ground tissues (obligate resprouters), and recruitment is produced in  
133 the intervals between fires (Keeley and others 2012), ii) plant mortality with  
134 survival of the seeds (obligate seeders) or iii) a combination of both mechanisms

135 (facultative shrub species; according to Pausas and others 2004 and Paula and  
136 Pausas 2008). Studies of post-fire dynamics have shown that plant communities  
137 dominated by resprouter species (which are usually late successional) are more  
138 resilient to both short and long fire intervals than communities dominated by  
139 seeder species (Keeley 1986), yet important questions remain on how the various  
140 plant functional types interact in shaping the post-fire community development.  
141 The resilience of pine forests to frequent fires is largely limited by pine seed  
142 production. This means that the occurrence of high recurrent repeated fires in a  
143 short interval of time or of a single fire in a young pine forest can cause the local  
144 eradication of pines (immaturity risk; Moreira and others 2011; De las Heras and  
145 others 2012). This eradication gives rise to the dominance of other species, which  
146 could either be early or late successional, depending on the species composition  
147 of the understory before the fire (Rodrigo and others 2004). In this context,  
148 several studies indicate that high wildfire frequency can favour the replacement  
149 of pine and oak forests by fire-prone shrublands (Acácio and others 2009, 2010;  
150 Santana and others 2010; Santana and others 2010, 2014). Furthermore, the  
151 colonization of late successional species, such as resprouter oak trees, in fire-  
152 prone shrublands can be limited by several factors related to seed dispersal and  
153 micro-climate conditions (Acácio and others 2007; Pons and Pausas 2007).  
154 These recruitment limitations could arrest successional processes, locking the  
155 system in a shrubland state, i.e. plant communities that lack a tree layer and are  
156 dominated by fire-prone shrub species (Acácio and others 2007, 2009, 2010;  
157 Santana and others 2010). The dominance of fire-prone shrublands can markedly  
158 reduce the resilience of the ecosystem by, for example, increasing erosion risk  
159 and decreasing biodiversity (Mayor and others 2016; Van del Elsen and others



160 2020). Despite this, oak tree species can also become dominant in former pine  
161 forests where pines have been eradicated as a result of recurrent fires (Keeley  
162 1986; Torres and others 2016, Baudena and others 2020).

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

181 According to Baudena and others (2020), pine forests will be replaced by oak  
182 forests in the long run. However, the post-fire resprouting ability of oak trees can  
183 be hampered because of unfavourable environmental conditions, e.g., due to the  
184 predicted climatic changes; this can, in turn, lead to the dominance of fire-prone

185 shrublands instead of late successional oak forests. Furthermore, we expect that,  
186 under high fire recurrence, oak tree dominance will be delayed by reduced seed  
187 colonization (low seed entry). We hypothesise that facultative resprouter shrubs  
188 will likely delay oak tree dominance further than obligate seeder shrubs because  
189 facultative species exhibit both a positive fire feedback due to their high  
190 flammability and a high persistence after fire due to their resprouting capacity. In  
191 short, whereas frequent fires in a short interval can deplete seed banks of obligate  
192 seeder shrubs, facultative shrub species can persist by their resprouting capacity,  
193 thus delaying their replacement by late successional species. According to this  
194 hypothesis, the main objective of this study was to improve our understanding of  
195 the role of facultative resprouter shrubs in delaying succession, represented by  
196 the dominance of oak tree species, following wildfire.

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

## 210 **Material and Methods**

211 We implemented a stochastic cellular automata model (also called interacting  
212 particle systems; Durrett and Levin 1994), which allowed representing spatial  
213 processes at the landscape scale. Cellular automata consist of one lattice, in  
214 which each cell acquires a discrete and finite value, and of transition rules that  
215 control the temporal and spatial changes in the values of the state of the cells  
216 (Wolfram, 1984). In our model, the state variable was the plant functional type.  
217 The lattice had 100\*100 cells (each cell being denoted by  $x$  in what follows), and  
218 each cell contained only one plant type, which could be interpreted as one adult  
219 tree but also of few small shrub plants. For simplification purposes, if the cell was  
220 considered as occupied by more plants, they were of the same type and age. The  
221 model considered three plant types ( $i=1-3$ ), each representing a different  
222 functional group with contrasting seed size, seed production and life span.  
223 Namely, we modelled pines ( $i=1$ ), either facultative or obligate seeder shrubs  
224 ( $i=2$ ) and oak tree ( $i=3$ ). The model species were inspired in *Genista* spp.  
225 (including formerly classified *Pterospartum tridentatum* (L.) Willk.) and *Ulex*  
226 *europaeus* L. for the facultative species, in *Erica umbellata* L., *Ulex*  
227 *parviflorus* Pourr. and *Salvia rosmarinus* Schleid. (formerly *Rosmarinus*  
228 *officinalis* L.) for the obligate seeder species, in *Pinus pinaster* Ait. for the pine  
229 and in *Quercus robur* L. for the oak tree ( Tavsanoğlu and Pausas 2018; Paula  
230 and others 2009). The model included additional information concerning the age  
231 of the plant cell when occupied and the number of seeds produced per cell, which  
232 corresponded to realistic values from literature (Fig. 1). The time steps used were  
233 of one year (i.e.  $dt=1$  yr). The simulations were performed by implementing a  
234 Matlab R2015b code.

## 235 **Soil seedbank**

236 We kept track of the soil seedbank  $SB_i$  at the plot scale (i.e., the whole lattice),  
237 for each plant functional type  $i$ , by computing both the production and the seed  
238 input from neighbouring areas. We assumed that the seeds were dispersed  
239 homogeneously across the plot, thus we multiplied each cell seed production  
240 rate,  $SP_i(x)$ , by the number of cells that were occupied by mature individuals in  
241 the whole lattice. For pines and shrubs, the average numbers of seeds per cell,  
242  $N_{seeds_{1,2}}(x)$ , were then calculated as the number of seeds in the soil seedbank,  
243  $SB_{1,2}$ , divided by the total number of cells. In the case of oak tree, given the small  
244 number of seeds compared to the other species, the seeds locally produced and  
245 those arrived from elsewhere were randomly distributed across the cells in the  
246 lattice to calculate  $N_{seeds_3}$ . In the following, we detail how we implemented seed  
247 production and storage in the seed bank.

### 248 *Seed production*

249 The annual pine seed production per cell  $SP_1(x)$  was estimated at 100 seeds,  
250 which was calculated by considering that 10% of the average produced seeds  
251 would be available for germination after predation and seed loss (Vega and  
252 others 2008). Pine age of maturity (AM, the age at which a tree starts, on average,  
253 producing seeds) was defined as 10 years, as an approximation of the values  
254 reported for *Pinus pinaster* (Tapias and others 2001, Thanos and Daskalaku,  
255 2000).

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

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

#### 264 *Seed Bank*

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

#### 278 **Litter accumulation**

279 The accumulation of litter was a spatially explicit process that took place in the  
280 cells occupied by a mature pine tree as well as in their surrounding eight cells  
281 (Moore neighbourhood). The litter content increased with an annual litter  
282 accumulation rate (Table 1), which was reduced to 20% of its value if the pines  
283 were not yet mature. The value obtained was the litter accumulation rate in the

284 cell that was occupied by a pine tree, while the eight neighbours of this cell  
285 received 50% of this value. In the model, each year, part of the litter was degraded  
286 (40%), so that for a monospecific plantation of pine, a maximum litter depth (6  
287 cm) was reached 20-30 years after pine plantation. All the litter values were  
288 based on field observations by experts.

### 289 **Transition rules: plant colonization and mortality**

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

295 Given the fact that the habitat conditions were equally suitable for all three  
296 species, the probability of establishment  $ProbS_i(x)$  of species  $i$  in a cell  $x$  was  
297 defined as a function of the seed number in the cell,  $Nseeds_i(x)$ , following Cannas  
298 and others (2003):  $ProbS(x) = 1 - \left(1 - \frac{1}{E_i}\right)^{Nseeds_i(x)}$ .  $E_i$  represented the number  
299 of seeds that under optimal conditions would guarantee the dominance of the  
300 species  $i$  in a cell. The values of  $E_i$  for the different species represented a  
301 competition factor for the seedlings, which considering the differences in seed  
302 size between species, was approximated to differ by a factor of 10 between the  
303 different species. This number was set to 2 for the oak trees, 10 for the pines,  
304 100 for the shrubs ( $i=2, 10, 100$ ). For the oak tree, this value was established at  
305 2 rather than 1, because the latter would lead to an establishment probability of  
306 almost 100%. The relations between the number of available seeds in a cell and  
307 the  $ProbS_i$  for each species are shown in Fig. 2.

308 Given the starting point of the system represented a pine plantation, the  
309 probability of establishment  $ProbL_i$  in an empty cell was expressed as a function  
310 of litter depth, as we assumed that the increasing litter thickness over time would  
311 favour the relative dominance of the late successional species and, at the same  
312 time, inhibit the colonization of the early successional species (Fig. 3; please see  
313 the equations in the appendix). More specifically, the effect of litter thickness was  
314 defined as depending on seed size and thus on species regeneration strategy  
315 and successional stage. These assumptions were based on the following  
316 arguments: i) bigger seeds typically do not present dormancy, whereas smaller  
317 seeds do and the breaking of this dormancy require fluctuations in temperature  
318 that do not occur when the litter layer is thicker than 1 cm; ii) bigger seeds have  
319 higher elongation potential than smaller seeds and, thus, can establish  
320 themselves successfully under greater litter depths and iii) bigger seeds are more  
321 susceptible to predation and/or desiccation than smaller seeds and, therefore,  
322 can benefit more from the protective effect of litter (both by hiding the seeds and  
323 by buffering climatic extremes). The values of the contribution due to litter depth  
324 to probability of establishment  $ProbL_i(x)$  for the three different functional types  
325 were based on the literature (e.g. Molofsky and Augspurger 1992; López-Barrera  
326 and González-Espinosa 2001; Fagúndez and Izco 2004; Kostel-Hughes and  
327 others 2005; Fernandes and Rigolot 2007; Giertych and Suszka 2011; Egawa  
328 and Tsuyuzaki 2013). Seed sizes for the different functional types were estimated  
329 as follows: the obligate seeder (e.g. *Cistus* spp.) and facultative (e.g. *Rosmarinus*  
330 *officinalis*) shrub species have small seeds (<0.50 mg per seed, Thanos and  
331 others 1992, Fagúndez and Izco 2004; Vasques and others 2012); the pine tree  
332 (e.g. *Pinus pinaster*) had intermediate size seeds (~54 mg per seed, Garcia-

333 Fayos 2001); the obligate resprouter tree (e.g. *Quercus robur*) had large seeds  
334 (2-6 g per seed, Garcia-Fayos 2001, Giertych and Suszka 2011). This information  
335 was complemented by author observations of the elongation potential of the  
336 different seeds during the cotyledon phase during germination experiments. See  
337 Fig.3 for the relations between litter depth and  $ProbLi(x)$  for each functional type.  
338 To decide which species will colonize a certain empty cell, we followed a standard  
339 approach to assign species to cells in proportion to the respective establishment  
340 probability. The species colonization probabilities in each cell were compared to  
341 a random number ( $r$ ) drawn from a uniform distribution between 0 and 3. If the  
342 random number was smaller than the probability of colonization of species 1  
343 ( $r < ProbC_1$ ), the cell was colonized by species 1. Otherwise, if the number was  
344 smaller than the sum of the probabilities of species 1 and 2  
345 ( $ProbC_1 \leq r < ProbC_1 + ProbC_2$ ), species 2 colonized the cell. Species 3 colonized if  
346  $ProbC_1 + ProbC_2 \leq r < ProbC_1 + ProbC_2 + ProbC_3$ , and otherwise the cell remained  
347 empty (Danet 2014).

348 The annual mortality rate ( $AMORate$ , of each species was defined as one over its  
349 life span (Baudena and others 2020).

## 350 **Fire**

351 Fire disturbance regime was defined stochastically, with the occurrence of fires  
352 expressed by an exponential distribution of return times (Kampen 1992; Baudena  
353 and others 2010). In order to study the response of the system to different fire  
354 frequency conditions, we selected three different average fire return times: seven,  
355 fifteen and thirty years, plus a scenario without fire. When a fire occurred, the  
356 species with resprouting ability (oak tree or facultative shrub species) continued  
357 to occupy the same cell, whereas pines and obligate seeder shrubs die. The fire



358 that was simulated was of high severity for which all the needles (crown) and litter  
359 (floor) were consumed.

### 360 **Model simulation settings**

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

369 The model was initialized with a range of different initial conditions (e.g., variable  
370 initial pine density, number of shrub seeds and variable annual acorn input; not  
371 shown). After learning that the model was mostly sensitive to the variation in  
372 yearly acorn input, the initial conditions for the model runs were then selected as  
373 follows: initial pine plantation interval: 4 cells between pines; 100 shrub seeds per  
374 cell (produced on site during the early development of the pine plantation),  
375 number of oak seeds (acorns) across the plot given by the annual input, which,  
376 to obtain a broad spectrum, was simulated at 1, 5, 50 and 200 seeds.

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

381 **Results**

382 In the absence of fire, the system attained a stochastically stable coexistence of  
383 the three plant types at steady state. This equilibrium was reached after about  
384 500-1000 years from the initial pine plantation state and included predominantly  
385 oak trees (~75%) with co-existing pines (~20%) and both shrub types (<5%) (Fig.  
386 4A-B).

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

396 The relative dominance of oak trees at steady state (i.e., cover values higher than  
397 50%) was maintained under all recurrence intervals of high-severity fires (Fig.  
398 4C-F). The coexistence of all three functional types, however, was not observed  
399 when fires were simulated, since pines went extinct in all fire regimes, because  
400 of a combination of seed bank depletion and a reduction in empty sites available  
401 for pine establishment. Under high fire frequency conditions, obligate seeder  
402 species were also eradicated from the system (average fire return time of 7 years;  
403 Fig. 4H). Nevertheless, when the facultative shrub species was included in the  
404 simulations, a long-term co-existence of shrub and oak trees was reached under  
405 all fire disturbance regimes (Fig. 4C,E,G). The time at which pine trees were

406 eradicated from the system depended exclusively on the fire return time (Fig.  
407 4C,E,G). Pine cover was eradicated (0% of cover) fastest at the highest fire  
408 frequency, namely we observe eradication times of about 40, 130 and 265 years,  
409 for fire frequency of 7, 15 and 30 years, respectively. These values did not change  
410 for different values of oak trees seed input or regeneration strategy of the shrub.  
411 However, the time at which oak trees reached dominance was not only  
412 dependent on fire frequency, but also on the resprouting capacity of the shrub  
413 (Fig 4C-H). In particular, high fire frequency accelerated oak tree dominance  
414 when the shrub was an obligate seeder but delayed it when the shrub had  
415 resprouting ability (facultative shrub species; Fig. 4C-H). This result was  
416 observed for all the input rates of oak tree seeds. However, oak tree dominance  
417 was delayed substantially (up to 550 years) when acorn input rates were very low  
418 (1 seed.year<sup>-1</sup>, Fig.5).

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

## 423 **Discussion**

424 We evaluated the role of plant characteristics, namely post-fire regeneration  
425 strategies of fire prone shrubs in influencing successional processes. Our model  
426 results indicated that the period of dominance of shrubs after fire is mostly  
427 dependent on their post-fire resprouting capacity, with a delay in succession  
428 caused by the resprouting capacity of the shrubs. This was due to spatial  
429 competition between species since a cell that is occupied by a resprouter shrub  
430 remained occupied after a fire, while a cell that was occupied by an obligate

431 seeder was empty after a fire. Field studies also suggested that the post-fire  
432 recovery of oak forests could be slow, with shrubland communities dominating in  
433 the first decades (Baeza and others 2007; Alvarez and others 2009). In short, we  
434 found that the facultative strategy (which regenerates both by seeds and  
435 resprouting) could delay succession for a considerable amount of time, in the  
436 order of centuries. This would likely lead to notable degradation, with increased  
437 erosion risk, reduced biodiversity, soil fertility, and potential for C sequestration  
438 (Mayor and others 2016; Van del Elsen and others 2020) and could be enhanced  
439 by climate change and aridity (Batllori and others 2017, 2019). In this context, the  
440 increase in the time of dominance of facultative shrub species that was observed  
441 in our model, highlights the importance of assessing the resprouter capacity of  
442 Mediterranean shrubs in response to recurrent fires.

443 In the absence of fire, our results showed a stable coexistence between shrubs,  
444 pines and oak trees. The time of species relative dominance related to their life  
445 span, in the sense that short lived species dominated earlier in the succession,  
446 whereas long lived species dominate later on, in agreement with the theory of  
447 initial floristic model of succession (Egler, 1954). The relative dominance of late  
448 successional oak tree, such as *Quercus robur*, in the Iberian Peninsula during the  
449 last ten thousand years was confirmed by paleobotanical records (Alcalde and  
450 others 2006). These records also suggested a long presence of *Pinus pinaster* in  
451 the Iberian Peninsula, prior to their widespread plantation by humans.  
452 Furthermore, sporadic fires might be favourable to pine communities, by creating  
453 open areas for pine colonization (López-Sáez and others 2010). Thus, the  
454 prevailing vegetation before intensive human impacts in the landscape probably  
455 consisted of a mixed pine-oak woodland and not of the typical climax vegetation

456 suggested by the phytosociological model of Rivas and Martinez (1987), in which  
457 the tree layer was exclusively composed of oak species (Alcalde and others 2006;  
458 López-Sáez and others 2010). As expected, in the absence of fire, no differences  
459 between different shrub strategies were found since for modelling purposes only  
460 differences in post-fire regeneration strategy were considered. Previous model  
461 studies confirmed that in the absence of fire, the vegetation was dominated by  
462 early successional species, mainly *Pinus* spp. and with the passage of time this  
463 vegetation became dominated by later successional tree species (*Quercus* spp.).  
464 However, when early successional communities were affected by recurrent fires,  
465 plant succession can be arrested or delayed through a positive flammability-fire  
466 feedback loop, hence hampering fire resilience (Baudena and others 2020). A  
467 single fire is sometimes enough to change *Pinus* spp. forests into alternative  
468 stable states dominated by shrub communities. This trajectory deviation is more  
469 likely under high fire frequency regimes where the vegetation changes to dwarf  
470 shrubs and herbs (Santana and others, 2010, 2014). In this line, post-fire  
471 recovery is expected to be faster in communities that are already dominated by  
472 oak trees before the fire than in communities that are dominated by pine or shrubs  
473 (Calvo and others 2003).

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

481 the age of maturity of the pines, i.e., 10 years (Eugenio and others 2006),  
482 however, the stochastic variations in fire return time that were simulated in the  
483 model (with a possibility for events of short fire recurrence intervals than the  
484 average frequency that is observed) can also be observed in nature.

485 According to our model results, oak trees also reached dominance under high fire  
486 frequency. In particular, oak trees were dominant at equilibrium in all the  
487 scenarios of fire disturbance, and this final outcome was not sensitive to changes  
488 in other model parameters, such as low acorn availability. These results agree  
489 with previous works (Baudena and others, 2020) that found oak tree dominance  
490 in the long-term independently of the regime of fire occurrence. This pattern can  
491 be explained by the very high resprouting ability and long-life span of oak trees.  
492 Conversely, the other species tend to lose dominance over time, either because  
493 of having a short life span (shrubs) or a regeneration strategy that depends on  
494 local seed banks (pine and obligate seeder shrubs). Our results also agree well  
495 with the initial floristic model of succession (Egler, 1954), according to which post-  
496 fire conditions tend to attain a similar state of equilibrium than the one that would  
497 be achieved in the absence of fire (Trabaud, 1987). Furthermore, previous field  
498 studies suggested that oak tree species generally resprout rapidly and vigorously  
499 after fire under a wide set of conditions (Espelta and others 2003, Pausas 1997).  
500 Similar results were found under a frequent fire regime (Lloret and others 2003;  
501 Konstantinidis and others 2005), even after a period as short as three years after  
502 the last fire (Delitti and others 2005). These studies concerned forests that were  
503 already dominated by oak tree species, so that colonisation by oak tree species  
504 was not a limiting factor. In many instances, however, oak tree seed sources are  
505 distant, and there are few oak stands in the region, leading to very low acorn

506 inputs from the surrounding areas, hence absolutely delaying the post-fire  
507 succession of pine forests (Acacio and others 2010; Urbieta and others 2010).  
508 Unfavourable environmental conditions for the regeneration of oak tree species,  
509 such as steep slopes and cold or dry sites have been previously linked to the  
510 persistence of pine populations, however such conditions were not simulated in  
511 our model (López-Sáez and others 2010). We have found that oak tree  
512 dominance under optimal conditions for oak establishment was accelerated by a  
513 higher yearly input of acorns, as expected. Previous research, however, has  
514 shown that the relative abundance of oak tree species depends strongly on their  
515 colonization potential and on the establishment success of oak seedlings  
516 (Sheffer, 2012). Our model showed that a very small initial oak tree population  
517 and a small but steady yearly supply of 1 or 2 acorns per hectare could lead to  
518 oak tree dominance within 200 years, at least in the absence of fire. This outcome  
519 was altered by frequent fire regimes, which led to a delay in oak tree dominance  
520 of a few centuries in cases of very low acorn supply (1 acorn per hectare per  
521 year). At yearly acorn supply values of 50 per hectare, frequent fire regimes no  
522 longer delayed oak tree dominance. In the field, acorn inputs strongly depend on  
523 the distance from seed sources, e.g., on the presence and distribution of mature  
524 oak trees in the landscape. Since a low seed input has shown to influence the  
525 speed of oak tree dominance, we can expect that, understanding and  
526 manipulating the potential and effective dispersal of oak trees to the area can  
527 increase the presence of oak trees in the landscape. To do this, the promotion of  
528 acorn dispersers, such as the jay (*Garrulus glandarius* L.) could be considered  
529 (Ouden and others 2005). In this context, it is important to note that the type of  
530 plant community species dominance can interact with the colonization capacity

531 of oak trees, as pine stands foster seed arrival, whereas shrublands are usually  
532 avoided by the jay because open areas usually lead to a higher exposure to  
533 predators (Pons and Pausas 2006). These mechanisms could inhibit oak tree  
534 colonization in highly dense shrublands, which could, in turn, lock the system in  
535 an early successional phase, especially when pines are eradicated from the  
536 system. This would agree well with the findings of Acacio and others (2007) who  
537 found seed arrival to be one of the limitations of oak tree establishment in  
538 shrublands.

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

554 The model presented here assumed resprouting behaviour of the main shrub  
555 species and the oak trees as a binomial feature, i.e., a species either does or



556 does not resprout after fire. However, it is presently known that post fire  
557 resprouting capacity is actually a continuum, in terms of both the individual and  
558 the community response to a disturbance (e.g. fire or herbivory) (Moreira and  
559 others, 2012, Nicholson and others 2017). In spite of the high relative abundance  
560 of resprouting species in several ecosystems around the globe and on their  
561 tendency to become numerous in less productive sites, a focus on the role of  
562 resprouters in community dynamics has been underrepresented in previous  
563 modelling and successional studies (Midgley 1996; Bond and Midgley 2001).

564 The plantation of extensive areas with pines in the Iberian Peninsula did not only  
565 target wood production interests, but also aimed to foster ecological succession,  
566 with pines as a pioneer species promoting the subsequent colonization by more  
567 resource-demanding late successional species (Zavala and others 2000).  
568 However, several studies have shown that, pine stands have largely failed to  
569 harbour late successional species, possibly because of their high planting  
570 densities (Maestre and Cortina 2004; Gavinet and others 2015). In this context,  
571 the use of mixed pine plantations including late successional species has been  
572 proposed to increase the resilience of pine forests to frequent wildfires as well as  
573 to foster and accelerate succession (Pausas and others 2004; Vallejo and others  
574 2009; Santana and others 2018). Our model results suggest that the composition  
575 of the understory of pine stands should be considered, in particular regarding the  
576 resprouting capacity of fire-prone shrubs, as it can play an important role in  
577 constraining successional processes after pine has been eradicated from the  
578 system. Further research on the post-fire competitive effect of other facultative  
579 species with invasive behaviour in Portugal, such as acacia (*Acacia* spp.) and  
580 *Hakea sericea* Schrader is needed since, according to our results, their potential

581 to delay the establishment of oak tree populations could be enhanced by their  
582 regeneration strategy.

### 583 **Conclusion**

584 Our model indicated that the final succession state of pine-oak tree-shrub  
585 ecosystems is not influenced by fire frequency. The steady state dominated by  
586 oak trees is nearly insensitive to differences in initial model conditions. However,  
587 the time until oak tree dominance was reached was strongly delayed by the post-  
588 fire resprouting ability of understorey shrub species. Our results showed the  
589 importance of considering the resprouting ability of understorey shrubs in the  
590 assessment and management of pine forests that are subject to frequent fires,  
591 as a high post-fire resprouting capacity could inhibit plant succession for several  
592 centuries, especially under low levels of acorn yearly input, which could, in turn,  
593 lead to extensive post-fire erosion and degradation.

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