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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**
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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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109 shrub-dominated succession stage for several centuries. Our simulation results

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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⁻¹, 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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