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Fire responses shape plant communities in a minimal model for fire ecosystems across the world --Manuscript Draft--

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1 **Title page**

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9

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21 **Abstract**

22 Across plant communities worldwide, fire regimes reflect a combination of climatic factors and
23 plant characteristics. To shed new light on the complex relationships between plant characteristics
24 and fire regimes, we developed a new conceptual, mechanistic model that includes plant
25 competition, stochastic fires, and fire-vegetation feedback. Considering a single standing plant
26 functional type, we observed that highly flammable and slowly colonizing plants can persist only
27 when they have a strong fire response, while fast colonizing and less flammable plants can display
28 a larger range of fire responses. At the community level, the fire response of the strongest
29 competitor determines the existence of alternative ecological states, i.e. different plant
30 communities, under the same environmental conditions. Specifically, when the strongest
31 competitor had a very strong fire response, such as in Mediterranean forests, only one ecological
32 state could be achieved. Conversely, when the strongest competitor was poorly fire-adapted,
33 alternative ecological states emerged, for example between tropical humid savannas and forests,
34 or between different types of boreal forests. These findings underline the importance of including
35 the plant fire response when modeling fire ecosystems, e.g. to predict the vegetation response to
36 invasive species or to climate change.

37

38

39 **1 Introduction**

40 Understanding the complex relationships between fire and its drivers is essential for both
41 predicting environmental change in fire-prone biomes and assisting in fire management practices.
42 Climatic drivers are generally used to predict fire frequency, fire season and burned area
43 (Westerling and Bryant 2008; Jolly et al. 2015; Abatzoglou and Williams 2016; Boer et al. 2016;
44 Ruffault et al. 2017; Turco et al. 2017, 2018). On the other hand, fire regimes, which include the
45 type, frequency, intensity, seasonality and spread of recurrent fires (Gill 1975; Turner et al. 1998;
46 Turner 2010), also depend on biological feedbacks (Thom and Seidl 2016; Pausas and Ribeiro
47 2017; Archibald et al. 2018; Pausas and Keeley 2019). Plant types influence fire primarily in terms
48 of the availability, continuity and flammability of fuel (Wells et al. 2004; Bowman et al. 2009;
49 Higuera et al. 2009; Karavani et al. 2018). Within each climate zone, plant characteristics can help
50 to explain the occurrence of different fire regimes in different biomes (Archibald et al. 2013;
51 Pausas and Ribeiro 2013). In tropical ecosystems, for instance, fast-growing and drying savanna
52 grasses encourage frequent and low intensity fires, thus preventing the growth of forest trees that
53 are poorly adapted to fires (Beckage et al. 2011; Ratnam et al. 2011). Such vegetation-fire feedback
54 has been suggested to preserve savannas in areas where a closed humid forest might be expected
55 based on climatic conditions alone (Van Langevelde et al. 2003; Bond 2008; Dantas et al. 2016;
56 D’Onofrio et al. 2018). Similar examples of fire’s role in maintaining ecological stability have
57 been shown in boreal (Johnstone et al. 2010; Rogers et al. 2015; Couillard et al. 2018; Abis and
58 Brovkin 2019) and temperate forests (Kitzberger et al. 2012, 2016; Tepley et al. 2016). Thus, fire
59 regimes involve several feedbacks between plants, fires and climate, at differing spatial and
60 temporal scales (Wright and Clarke 2007; Ali et al. 2008; Pausas and Keeley 2009; Johnstone et
61 al. 2010; Archibald et al. 2018; Karavani et al. 2018).

62

63 In fire-prone environments, plant communities are shaped both by community dynamics, such as
64 competition, and by fires (Lavorel and Garnier 2002). These factors are reflected in plant traits
65 (Reich et al. 2003), including multiple types of plant adaptations to the local fire regime (Keeley
66 1986; Gignoux et al. 1997; Keeley et al. 2011). The traits that allow a species to survive within a
67 particular environment are often correlated, creating so-called trait “syndromes” (Reich et al. 2003;
68 Archibald et al. 2018). In addition, for a given species, plant traits and trait syndromes reflect the

69 trade-off between strategies (Grime 1977; Chapin III et al. 1993). For instance, tropical forest trees
70 invest resources in fast growth between fire events (Rossatto et al. 2009; Viani et al. 2011) rather
71 than investing in individual plant protection from fire damages (Hoffmann et al. 2012; de L. Dantas
72 et al. 2013).

73
74 Among fire-adapted species, three fire syndromes can be identified (Pausas 2015a). These
75 correspond to species that survive fires either at individual or at population level, or to species that
76 do not tolerate fires. Plants that cope with fire at individual level (also named ‘fire resisters’, or
77 ‘fire survivors’ in Schwilk and Ackerly 2001) may have thicker bark, which limits the damage to
78 the tree during relatively low intensity, surface fires (Keeley et al. 2011), or may readily re-sprout
79 after intense fires thanks to large below-ground carbohydrate reserves (Gignoux et al. 1997; Bond
80 and Midgley 2001). Species that survive fires at population level (also called ‘fire embracers’)
81 generally have elements of their life cycle closely tied to fire, including germination caused by
82 combustion, post-fire seed release in crown systems (serotiny) or enhanced flammability to
83 increase the frequency and intensity of fires to the detriment of non-resprouting competitors
84 (Schwilk and Ackerly 2001; Keeley et al. 2011). Finally, fire-intolerant species (or ‘fire avoiders’)
85 may have few adaptations to fire and are generally found in areas where fires are infrequent (Pausas
86 2015a).

87
88 In this study, we use a newly developed conceptual model (*sensu* Robinson 2008a, 2008b) to
89 investigate the emergence of different plant communities in consequence of plant-fire interactions
90 and plant competition for resources. We classified plants into functional types (PFTs), defined in
91 terms of plant structure, response and functioning that are related to different sets of traits (Box
92 1996; Pausas and Lavorel 2003; Lavorel et al. 2007). This minimal model was a convenient
93 framework for highlighting the general conceptual relationships between fires, plant characteristics
94 and community composition. Similar approaches have been developed for specific biomes, such
95 as savannas (Beckage et al. 2009, 2011; Baudena et al. 2010; De Michele et al. 2011; Ratajczak et
96 al. 2011; Staver and Levin 2012), the Mediterranean basin (Batllori et al. 2015, 2019; Baudena et
97 al. 2020) and boreal communities (Abis and Brovkin 2019), but none of them encompasses
98 ecosystems throughout different biomes, with the notable exception of the seminal work of
99 (Casagrandi and Rinaldi 1999).

100

101 In this work, we addressed the following research questions:

102 (RQ1) What set of characteristics can lead an individual PFT to persist, in isolation, for different
103 emerging fire regimes?

104 (RQ2) Which are the main plant characteristics, if any, that influence the emergence of different
105 communities?

106 (RQ3) What combination of plant characteristics can lead different plant communities to emerge
107 as alternative ecological states?

108

109 **2 Methods**

110 *2.1 Model*

111 We developed a new conceptual model to describe the dynamics of fire-prone plant communities.
112 Then, we numerically integrated the model equations, and we performed parameter sensitivity
113 analyses to answer the three research questions listed above. This model is a generalization of the
114 approach of Baudena et al. (2020), developed for Mediterranean forests.

115

116 We distinguished the PFTs by their main characteristics, focusing in particular on competitive
117 ability (mostly representing shade tolerance), fire response (encompassing several traits from
118 individual to PFT level) and vegetation flammability (here driving fire occurrence). These
119 characteristics are represented and quantified by specific parameters. Here, the fire responses
120 included both the resistance of individual plants during fire, e.g. due to a thick bark, and the post-
121 fire recovery strategies at individual or population level, such as resprouting ability or the existence
122 of a large, persistent and fire-resistant seedbank (Pausas and Keeley 2019; Miller et al. 2020).

123

124 In the model, each community was composed of three PFTs, which represent the most relevant
125 plant types in a given ecosystem. We chose to limit the number of parameterized PFTs to three as
126 a compromise between detail and parsimony, following the examples of e.g. Staver and Levin
127 (2012), Abis and Brovkin (2019), and Batllori et al. (2015) for specific biomes. The model is
128 space-implicit, i.e. it simulates the plant cover dynamics within an area (of the order of 100x100
129 m²) where the seeds of the PFTs are assumed to be able to disperse homogeneously. Two factors

130 drive the assembly dynamics: plant-plant competition (Sec. 2.1.1) and fire (Sec. 2.1.2). During
 131 fire-free periods, PFTs succession is regulated by plant competition for resources (mostly light in
 132 this work), following the approach of Levins (1969), Hastings (1980) and Tilman (1994). The
 133 (deterministic) succession is perturbed by fires, which are represented as stochastic events and
 134 occur in pulses. At each time, the chance of fire occurrence depends on the flammability of the
 135 community. In turn, different plant responses to fires lead to different post-fire community
 136 compositions. These two interactions create the fire-vegetation feedback in the model.

137

138 *2.1.1 Competition model*

139 Between two consecutive fires, the dynamics of the system is governed by three ordinary
 140 differential equations (Tilman 1994) for the variables b_i ($i=1,2,3$), which represent the fraction of
 141 space occupied by PFT_{*i*} ($0 \leq b_i < 1$),

142

$$\frac{db_1}{dt} = c_1 b_1 (1 - b_1) - m_1 b_1 \tag{1}$$

$$\frac{db_2}{dt} = c_2 b_2 (1 - b_1 - b_2) - m_2 b_2 - c_1 b_1 b_2 \tag{2}$$

$$\frac{db_3}{dt} = c_3 b_3 (1 - b_1 - b_2 - b_3) - m_3 b_3 - c_1 b_1 b_3 - c_2 b_2 b_3, \tag{3}$$

143

144 where t represents time (in years, yr). Parameters m_i are the plant mortality rates (yr^{-1}), while c_i
 145 are the colonization rates (yr^{-1}), that represent the combined processes of seed production,
 146 germination, and establishment. Finally, $1 - \sum_i b_i$ is the amount of empty space. Each plant type
 147 can colonize both the empty spaces and the space occupied by the inferior competitors, where $c_i b_i$
 148 is the fraction of space that PFT_{*i*} can colonize per time unit. A fixed hierarchy between PFTs was
 149 assumed, from the strongest ($i = 1$) to the weakest ($i = 3$) competitor, corresponding to an inverse
 150 successional order (i.e., from late to early). The fractional cover of each PFT corresponds to the
 151 field cover in real ecological settings, which includes different layers, and is normalized to the
 152 total area of the layers. In the absence of fires, the plant community reaches a stationary state that
 153 can be easily determined (Tilman 1994).

154

155 2.1.2 Fires

156 Fires are modeled as instantaneous, stochastic events. These are represented by a nonstationary
157 Poisson process: the average fire return time T_f (yr) is exponentially distributed, and the process
158 is “non stationary” because the average return time is state dependent (following e.g. D’Odorico
159 et al. 2006), i.e. the value of T_f changes across the simulation depending on the present community
160 composition (see also Appendix C). As we consider a set climate in each ecosystem, the average
161 fire return time is assumed to depend only on fuel availability and community composition, taking
162 into account the different PFT flammabilities, as follows

$$T_f = \frac{1}{\sum_{i=1}^3 b_i L_i}. \quad (4)$$

163 Hence, a larger plant flammability, L_i , determines more frequent fires. Similarly, abundant fuel
164 (represented by large vegetation cover values, b_i) and in particular, a greater cover of the more
165 flammable PFTs, decreases the average fire return time, thus leading to a higher chance of fires
166 (D’Odorico et al. 2006; Baudena et al. 2010, 2020). The ecosystem is assumed to be fuel-limited,
167 but not ignition-limited.

168

169 Since the exponential distribution of fire return times could lead to extremely frequent fires, we
170 set the minimum fire return time, T_f^{min} , to 1 or 2 years, depending on the target ecosystem (see
171 Table 1). This represents the time needed for a (partial) recovery of the ecosystem after fire, since
172 burned ecosystems are not immediately prone to new fires. For numerical purposes, we also set
173 the maximum fire return time to $T_f^{max} = 10^4$ yr.

174

175 At each fire event, the cover of each PFT $_i$ is instantly reduced, retaining only a fraction, R_i (between
176 0 and 1), of the original cover before fire. The parameter R_i , called ‘fire response’ hereafter,
177 accounts for different processes and plant strategies that can have complementary roles for PFT
178 survival, including fire-related plant mortality and plant recovery strategies after fire. Following
179 (Pausas and Lavorel 2003) we rated fire response strategies, assuming that strategies ensuring
180 individual survival were more efficient (high R_i) than strategies resulting in PFT survival but
181 individual loss after fire (intermediate R_i). For crown fires, which often completely burn the
182 aboveground biomass, R_i represents the efficiency of post-fire regrowth, due to resprouting or
183 seedbank germination (Clarke et al. 2005, 2013). For surface fires, this parameter represents the

184 persistence of plants during fire, e.g. thanks to a thick bark (Lawes et al. 2011; Pausas 2015b). In
185 either case, the parameter R_i rated the fire response of a PFT to the typical fire regime observed in
186 the ecosystem where that PFT occurred. In this representation, the fire response parameter R_i not
187 only described the ability of plants to survive fires, but also implicitly included fire intensity,
188 because it represented the severity of the fire and the strength of the response of a PFT to the
189 typical fire activity of a certain geographical area. For simplicity, within a certain area, all fires
190 were considered to have the same intensity, while across areas they could be different (e.g.
191 typically crown fires in the Mediterranean and low-intensity surface fires for the savannas;
192 Archibald et al. 2018).

193

194 Equation (4) and the fire response representation introduce a feedback between the probability of
195 fire occurrence and the composition of the plant community: plant cover, which is affected by fires
196 via R_i , in turn determines fire occurrence. As a consequence, we expect that in this model different
197 fire histories occurring in an ecosystem may result in alternative ecological states, characterized
198 by dissimilar communities (D’Odorico et al. 2006; Baudena et al. 2010; Kitzberger et al. 2012;
199 Staver and Levin 2012).

200

201 We also defined a non-dimensional version of the model (see Appendix A for the explicit
202 derivation), which allowed us to interpret the results obtained for RQ1. This non-dimensional
203 model corresponds to a Lotka-Volterra’s competition model, with null bottom-up competition, i.e.
204 negligible effect of the weaker competitors on the stronger ones (Chesson 2000; Kot 2001;
205 Rauschert and Shea 2017).

206

207 *2.2 Analyses*

208 Before addressing the research questions, we performed a general analysis of the model dynamics,
209 investigating the community composition and plant cover achieved in the absence of fires; we then
210 activated the fire dynamics and assessed the long-term community structure and the possible
211 presence of multiple, alternative ecological states.

212

213 To answer the research questions, the analyses included two parts: (i) ‘PFT characteristics’
214 (corresponding to RQ1), where we analyzed how the characteristics (i.e., the model parameters)

215 of an individual PFT in isolation related to each other, and how these characteristics related to the
216 resulting fire frequency in fire-prone environments; (ii) ‘Community emergence’ (corresponding
217 to RQ2-3), where we assessed which characteristics, if any, of the PFTs present in a certain biome
218 related to the emergence of different communities, possibly leading to alternative ecosystem states.
219 To these ends, we explored the parameter space by running 50 simulations for each set of
220 parameters, i.e. one point in the parameter space (see Sections 2.2.1 and 2.2.2.2), to capture the
221 variability in cover due to the stochastic fire dynamics and initial vegetation cover. All simulations
222 were run for 15,000 yr to ensure that the variability in vegetation cover generated by fire
223 stochasticity was fully captured. We notice here that plant dynamics had much shorter time scales
224 (see e.g. Fig. 1): in the ‘Community emergence’ analyses, the long-term ecological state was
225 usually achieved in 100-1,000 yr for all the case studies considered; the convergence time was
226 even shorter in the ‘PFT characteristics’ simulations.

227

228 *2.2.1 PFT characteristics*

229 First, we studied the plant characteristics that can lead an individual PFT to persist in isolation,
230 and the connections between these characteristics and the resulting fire frequencies (RQ1). To this
231 end, we modeled the dynamics of a single PFT, by setting the cover of the other PFTs to zero. For
232 these analyses we dropped the subscript i for all the variables and parameters since only one PFT
233 was considered in each simulation.

234

235 We generated random values of plant colonization rate, c , between 0.001 yr^{-1} and 20 yr^{-1} , and for
236 each of these we considered four values of the mortality rate, m , such that $c/m = [2, 5, 10, 20]$.
237 Then, for each combination of colonization and mortality rate, we varied the fire response, R ,
238 between 0.05 and 0.9 in steps of 0.05, and the flammability, L , between 0.001 yr^{-1} and 0.99 yr^{-1} ,
239 increasing its value by 1.5 times at each step. Finally, for each parameter set, we run 50 different
240 simulations by randomly varying the initial vegetation cover between 0.01 and 0.99.

241

242 We used the resulting average vegetation cover, $\langle b \rangle$, as an indicator of the success of the PFT
243 with the selected combination of R , L , c and m . Since each fire event reduced the PFT cover, which
244 instead grew between fires, we chose to compute the average vegetation cover of each simulation
245 by using only the value right before each fire event in the last 20% of the total simulation time.

246 For each parameter set, these values were then averaged across all the 50 runs. The same procedure
247 was applied to compute the average fire return time, $\langle T \rangle$, i.e. the average time between subsequent
248 fires, representing the fire regime in our model. In Appendix A, we discuss how the non-
249 dimensional version of the model helps interpreting the results.

250

251 2.2.2 *Community emergence*

252 The second set of simulations was designed to assess the effect of plant characteristics in shaping
253 plant communities (RQ2&3). We included three PFTs in this set of simulations, thus running the
254 full model described in Sec. 2.1. To parameterize the model, we focused on three plant
255 communities observed in different biomes where wildfires play a recognized role: Mediterranean
256 forests and shrublands, tropical humid savannas and forests, and boreal forests. See Table 1 for a
257 summary of the chosen plant types and their characteristics.

258 2.2.2.1 *PFTs and parameter settings*

259 The hierarchy among the PFTs was established by considering juvenile and adult shade tolerance.
260 The most competitive PFT₁ was usually a plant that can grow under scarce light availability. The
261 PFT₂ could not survive at very low light levels but persisted more easily than the PFT₃ in partially
262 shaded environments. The weakest competitor PFT₃ was affected by the shade of the other PFTs.
263 The three PFTs in the three case studies were identified as follows.

264

265 We focused on the Mediterranean Basin as a representative example of the Mediterranean biome.
266 We followed Baudena et al. (2020) in choosing Holm oak, *Quercus ilex*, as the most competitive,
267 late successional PFT₁ (Acácio et al. 2007; Amici et al. 2013; Vayreda et al. 2016). The PFT₂
268 represented pine species, such as Aleppo pine, *Pinus halepensis*, and Brutia pine, *Pinus brutia*
269 (Zavala et al. 2000; Zavala and Zea 2004), which are less shade tolerant than oaks. For the PFT₃
270 we chose a generic Mediterranean shrub seeder, simplifying from (Baudena et al. 2020) to
271 represent a mix of *Rosmarinus*, *Cistus* or *Ulex* spp.

272

273 For the humid tropical regions, we simply captured the contrast between shade-tolerant, fire
274 avoider rainforest trees (PFT₁) and shade-intolerant, fire resistant savannas, represented by

275 savanna trees (PFT₂) and savanna C4 grasses (PFT₃) (Staver and Levin 2012; Charles-Dominique
276 et al. 2018).

277

278 For boreal ecosystems, we focused on North American boreal species. We identified the shade
279 tolerant balsam fir, *Abies Balsamea* (Uchytil 1991a) as PFT₁, and the less shade tolerant, but very
280 common black spruce, *Picea mariana*, and jack pine, *Pinus Banksiana*, as PFT₂ (Carey 1993; Fryer
281 2014). These two latter species are similar in both shade tolerance and fire response. In the
282 following we will refer to PFT₁ and PFT₂ as the fire avoider conifer and fire embracing conifer,
283 respectively. The parameters estimated for balsam fir can also represent white spruce, *Picea glauca*
284 (de Lafontaine and Payette 2010, 2012), which is a late successional, fire avoider conifer tree
285 mostly found in western NA, where balsam fir is rare. Finally, shade intolerant deciduous
286 broadleaved trees (Girardin et al. 2013) were chosen as PFT₃; specifically, we parameterized PFT₃
287 considering paper birch, *Betula papyrifera* (Uchytil 1991b), and trembling aspen, *Populus*
288 *tremuloides* (Howard 1996).

289

Table 1. Characteristics of each PFT in the three case studies: Mediterranean, Tropical and Boreal North America biomes.

Biomes and location	Mediterranean forest and scrubs (Mediterranean basin)		
PFT identification	PFT₁: <i>Quercus ilex</i>	PFT₂: <i>Pinus</i> spp.	PFT₃: <i>Rosmarinus officinalis</i> , <i>Cistus</i> spp., <i>Ulex</i> spp
Shade tolerance	High: late-successional, broad-leaved evergreen	Medium: outcompeted by <i>Quercus ilex</i> (in mesic conditions)	Low: shrubs and perennial grasses outcompeted by trees
Fire response	Strong: high individual fire resistance, resprouts readily after fires	Intermediate: resistance at population level, post-fire seed release, serotinous cones in some species, thin juvenile bark, cones destroyed by severe crown fires, seedbank not produced in case of frequent fires preventing pines to reach maturity	Intermediate: shrubs: seeders with large seed banks and gradual seedbank decay, affected by ground fires; <i>B. retusum</i> : resprouter grass
Flammability	Low: moist and cool understory, very little fine and dead standing fuel, infrequent fires, average fire return time of 500 yr	Intermediate: vertical continuum fuel, flammable litter accumulation on the ground owing to summer senescence of needles, average fire return time of ~50yr	High: average fire return time of ~10yr
References	(Acácio et al. 2007; Puerta-Pinero et al. 2007; Saura-Mas et al. 2009; Timmer et al. 2009; Baeza et al. 2011; Amici et al. 2013; Azevedo et al. 2013; Clarke et al. 2013; Zeppel et al. 2015; Vayreda et al. 2016; Baudena et al. 2020)		
	(Pausas 1999a, 1999b; Zavala et al. 2000; Zavala and Zea 2004; Rodrigo et al. 2007; Climent et al. 2008; Fernandes et al. 2008; Karavani et al. 2018)		
	(Hanes 1971; Baeza et al. 2006; Acácio et al. 2009; Santana et al. 2010; Acácio and Holmgren 2014)		

Biomes and location	Tropical savanna and forest			Boreal forest (North America)		
PFT identification	PFT₁ : Forest trees	PFT₂ : Savanna trees	PFT₃ : C4 grasses	PFT₁ : <i>Abies balsamea</i> , <i>Picea glauca</i>	PFT₂ : <i>Picea mariana</i> , <i>Pinus Banksiana</i>	PFT₃ : <i>Betula papyrifera</i> , <i>Populus tremuloides</i>
Shade tolerance	High : broad leaved	Medium-Low : juvenile light sensitivity	Low : grows in canopy gaps or coexists with trees having low brunch density (e.g. savanna trees)	High : late successional trees	Intermediate : replaced by late successional species	Low : pioneer species, rare in late successional communities, can grow in forest canopy gaps
Fire response	Weak : low resistance at PFT level, fire-sensitive trunk	Strong : resistance at individual level, thick bark, survive to frequent ground fires	Strong : resistance at individual level, strong resprouters	Weak : low resistance at PFT level, avoider, seeder, seeds often destroyed by fires, survival trough unburned adult trees	Intermediate : high resistance at PFT level, embracer, semi-serotinous cones	Strong : high resistance at individual level, resister, resprouts form root collar when killed by fires
Flammability	Low : humid and shady understory, infrequent fires, average fire return time of ~1000yr	High : frequent fires, average fire return time of 3-5yr	High : fast-spreading ground fires occurring possibly every year	Low : fires almost absent in <i>Abies b.</i> forests, average fire return time of 250-300yr	Intermediate : layered structure, resinous wood, average fire return time of ~75yr	Low : high canopy moisture content, infrequent fires, average fire return time ~100yr
References	(San José and Farinas 1991; Kurokawa et al. 2003; Laurance et al. 2004; Russell-Smith et al. 2004; Bampfylde et al. 2005; Rossatto et al. 2009; Geiger et al. 2011; Viani et al. 2011; Hoffmann et al. 2012; de L. Dantas et al. 2013; D’Onofrio et al. 2018)	(Beckage et al. 2009; Warman and Moles 2009; Accatino et al. 2010; Baudena et al. 2010; Lehmann et al. 2011; Hoffmann et al. 2012; de L. Dantas et al. 2013)	(Accatino et al. 2010; Baudena et al. 2010)	(Rowe and Scotter 1973; (Viereck 1983; Payette 1992; Uchytill 1991a; Galipeau Carey 1993; Larsen 1997; et al. 1997; Sirois 1997; Greene and Johnson 1999; Bergeron 2000; Ali et al. 2000; Amiro et al. 2001; Wirth 2005; Ali et al. 2008; de Lafontaine and Bouchard et al. 2008; de Lafontaine and Payette 2010; Couillard et al. 2012; Johnstone et al. 2010, 2020; Payette et al. 2012; Fryer 2014; Abrahamson 2014; Rogers et al. 2015)	(Rowe and Scotter 1973; (Viereck 1983; Payette 1992; Uchytill 1991a; Galipeau Carey 1993; Larsen 1997; et al. 1997; Sirois 1997; Greene and Johnson 1999; Bergeron 2000; Amiro et al. 2000; Amiro et al. 2001; Wirth 2005; Ali et al. 2008; de Lafontaine and Bouchard et al. 2008; de Lafontaine and Payette 2010; Couillard et al. 2012; Johnstone et al. 2010, 2020; Payette et al. 2012; Fryer 2014; Héon et al. 2014; Rogers et al. 2015; Couillard et al. 2018; Hart et al. 2019, 2019)	(Swain 1980; Uchytill 1991b; Zasada 1992; Payette 1993; Howard 1996; Larsen 1999; Greene and Johnson 1999; Bergeron 2000; Brassard and Chen 2006; Bouchard et al. 2008; Bergeron and Fenton 2012; Rogers et al. 2013; Hart et al. 2019; Mack et al. 2021)

292 The parameter values for each PFT (Table 2) were estimated as follows. Given the intrinsic
293 ecological uncertainties in determining the parameter values, these were not intended to be exact
294 values but rather as reference values, around which we performed the sensitivity analyses. See
295 Appendix B for a detailed description of the PTF characteristics.

296 *Mortality rate.* We estimated mortality rates for each PFT as three times the inverse of the PFT
297 average lifespan in the absence of competition and fires: if colonization is inhibited, plant cover
298 decays exponentially, i.e. $b = b_0 e^{-mt}$, thus reducing to 0.05 b_0 within the average lifespan of the
299 species.

300 *Colonization rate.* These parameters were defined following published estimates, together with
301 additional information about growth time, spread rates and time needed to achieve a steady state
302 after almost total plant burning (see Table B1 in Appendix B and references therein).

303 *Flammability.* We considered the typical fire return time in communities where the PFT
304 represented the prevailing cover. When the domain is entirely covered by a certain PFT_{*i*}, eq. (4)
305 gives $L_i = 1/T_f$ (since ε is negligible), which defines the flammability as the inverse of the
306 average fire return time in an ecosystem dominated by PFT_{*i*}.

307 *Fire response.* We classified plants into three main categories, having weak, intermediate and
308 strong fire response (Pausas and Lavorel 2003; Jaureguiberry and Díaz 2023), which corresponded
309 to different ranges of R_i . We used information on bark thickness, serotiny, post-fire resprouting
310 strategies and rate of survival to frequent and intense fires to estimate this parameter. The range
311 $0 < R_i < 0.3$ represented plants that do not have fire response strategies neither at plant nor at PFT
312 level (i.e. fire avoiders); $0.3 < R_i < 0.7$ represented PFTs that do not display adaptations promoting
313 individual adult survival, but have an extensive seed bank that survives fires allowing plant
314 survival at PFT level (i.e. fire embracers); finally, $R_i > 0.7$ corresponded to plants having high
315 individual fire resistance, due for example to resprouting ability or thick bark (i.e. fire resisters).

316

317 *Table 2. Reference parameter values of colonization rate (c_i), mortality rate (m_i), flammability (L_i) and*
 318 *fire response (R_i) of PFT_{1,2,3} as parameterized for Mediterranean, tropical and boreal communities.*
 319 *Possible ranges identified in the parameterization (Appendix B) are reported in parentheses.*

Parameter	Mediterranean	Tropics	Boreal	Units
c_1	0.047	0.20 (>0.15-2.50)	0.085	yr ⁻¹
c_2	0.053	0.15 (0.15-2.50)	0.13	
c_3	0.3	20 (20-200)	0.17	
m_1	0.0025	0.01	0.035	yr ⁻¹
m_2	0.008	0.06 (0.03-0.3)	0.015	
m_3	0.03	3 (1-3)	0.023	
L_1	1/500	1/1000	1/250	yr ⁻¹
L_2	1/20	1/5	1/75	
L_3	1/10	½ (½-1)	1/100	
R_1	0.85 (0.80-0.90)	0.10 (0.10-0.30)	0.05 (0.05-0.20)	-
R_2	0.40 (0.30-0.50)	0.70 (0.60-0.80)	0.55 (0.4-0.6)	
R_3	0.50 (0.40-0.60)	0.85 (0.75-0.95)	0.85 (0.8-0.9)	

320

321 2.2.2.2 Parameter sensitivity analyses

322 To answer RQ2&3, we performed a parameter sensitivity analysis, i.e. we explored the type of
 323 communities that emerged across the parameter space. The model includes twelve parameters
 324 (excluding the two small thresholds, ε and δ) and, among them, only the fire response (R_i) has a
 325 defined, limited range of variability. Hence, the corresponding parameter space is a potentially
 326 infinite hypervolume. We limited the parameter space to exclude unrealistic parameter
 327 combinations and explored it around the reference values identified for the real communities in
 328 the three case studies described in Section 2.2. Fire responses, R_i , were varied in the range 0.01-
 329 0.90 in steps of 0.02, while c_i , m_i and L_i , were varied in a realistic broad range, from 0.5 to 2 times
 330 the reference value (flammability was increased by 1.05 its value at each step, while colonization
 331 and mortality rates were varied dividing the explored range into 40 steps). Colonization rates c_i

332 were always chosen to be larger than the mortality rates m_i to ensure plant survival in isolation
333 without fire (Tilman, 1994).

334

335 For each parameter set, we ran 50 simulations with different initial vegetation cover of the PFTs
336 included in the community. We ensured that the total initial vegetation cover of the three PFTs
337 was $\sum b_i \leq 1$ (Tilman 1994), by generating three random numbers in the range between 0.01 and
338 0.99, and then dividing each of them by their sum. The values thus obtained were arbitrarily
339 assigned to the three PFTs. These runs allowed us to: i) account for the variability due to fire
340 stochasticity; ii) observe all of the possible communities that could be achieved for a certain set of
341 parameters owing to the fire-vegetation feedback (i.e. the fire return time changed as a function of
342 the vegetation cover and community composition, possibly resulting in different trajectories, and
343 leading to alternative ecological states). Hence, the community can be reset by fire and change
344 thereafter owing to the plant succession. In each run, we recorded the community composition
345 before every fire event in the last 20% of the simulation time (15,000 y), considering only the PFTs
346 that had $b_i \geq 0.03$. This procedure was especially relevant in case of recurrent alternance between
347 different communities along the time series. We thus obtained a compilation of the possible states
348 (i.e., communities) achieved in the time series, for each parameter set.

349

350 To answer RQ2, we varied the parameters of each PFT, changing one parameter value at a time.
351 In the explored range, the parameters associated with the largest community changes with respect
352 to the reference were interpreted to be the plant characteristics that were most relevant for
353 determining the system state (i.e. the community composition).

354

355 Concerning RQ3, we explored parameter-space sections obtained by varying selected couples of
356 parameters among the most relevant ones (in the sense of the analysis described above), while
357 keeping all other parameters at their reference value. This allowed us to identify the parameters
358 that were most relevant for determining the existence of multiple alternative ecological states.

359

360 Finally, in a subset of the simulations, we accounted for the possible arrival of seeds from
361 surrounding areas (e.g., due to wind or animal transport), preventing a certain PFT from

362 disappearing after fire. We thus set a minimum post-fire vegetation cover $\delta \simeq 10^{-4}$, representing
363 germination of seeds coming from outside the study area.

364

365 **3 Results**

366 *3.1 PFT characteristics*

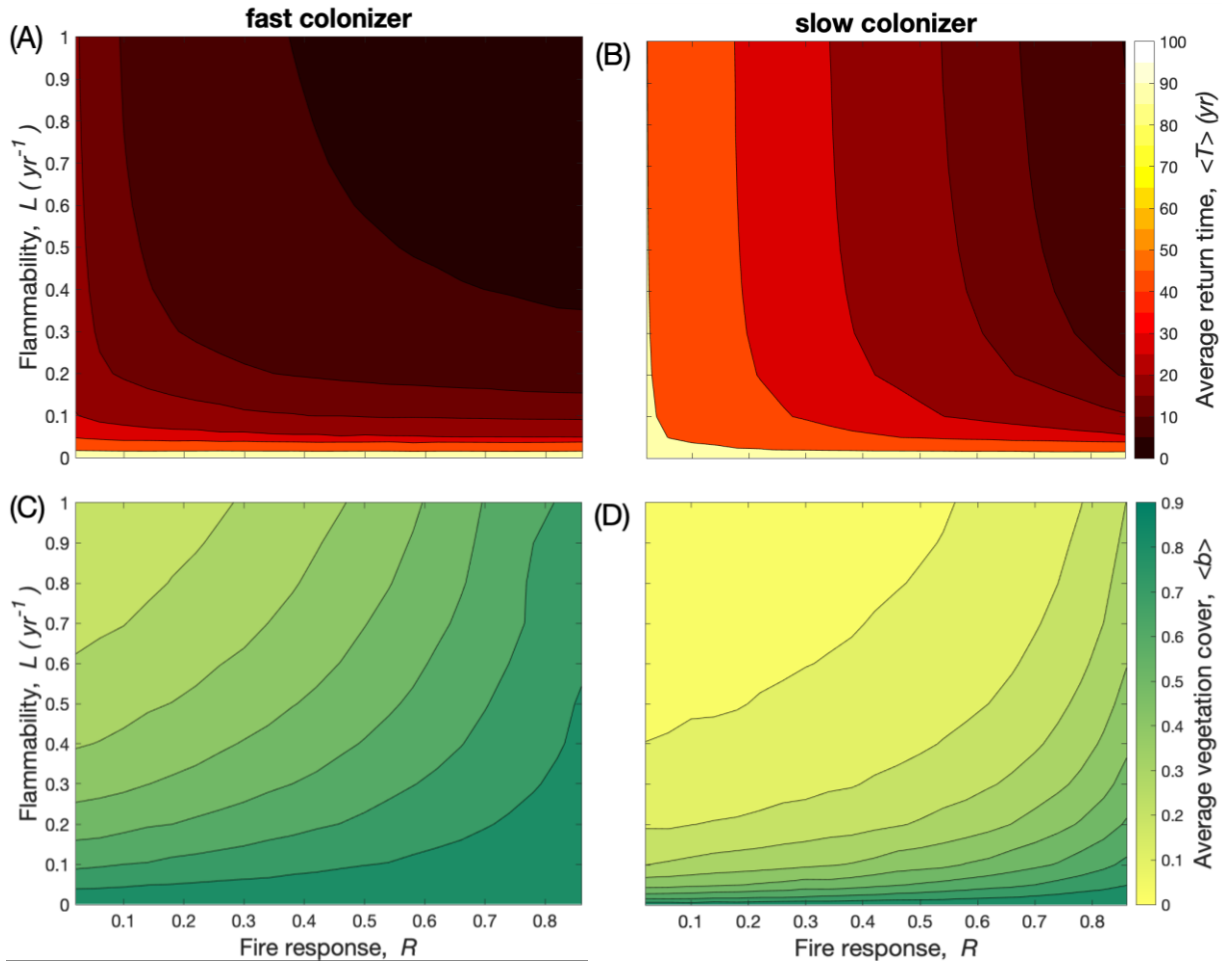
367 We first examined the dynamics of a single PFT. In this set of simulations and in the explored
368 parameter range, the system displayed only one final state (i.e., multi-stability, corresponding to
369 either a vegetated or not vegetated state, was never observed). When fires substantially reduced
370 the plant cover (e.g., at low fire response values), the average fire return time rose (Figure 1A-B)
371 owing to the fire-vegetation feedback, which allowed the PFT to re-establish itself. Therefore, we
372 never observed the total die out of the PFT.

373

374 To answer RQ1, we used two illustrative examples of PTFs with either high (0.3yr^{-1} , Fig 1a,c) or
375 low (0.05yr^{-1} , Fig. 1b,d, right panels) colonization rate c (mortality rate was $m=0.1c$); similar
376 results were obtained for other combinations of colonization and mortality rates (as described in
377 Sec. 2.2.1). When the plant flammability L was low, fires were rare ($\langle T \rangle$ of 100 yr or larger,
378 Figure 1A-B, light areas), and the average PFT cover was similar to its equilibrium value in the
379 absence of fires ($\langle b \rangle$ close to 0.9 in both examples, Figure 1C-D, dark areas) for any fire response
380 R . On the other hand, when the flammability was high, both the fire interval (upper half of Fig.
381 1A-B), and the average cover (upper half of Fig. 1C-D) depended on the specific fire response of
382 the plant. The average cover of fire intolerant (low R) and highly flammable PFTs was strongly
383 reduced by the resulting regime of frequent fires (top-left corners of Fig. 1A-B and Fig. 1C-D). In
384 contrast, frequent fires only slightly reduced the cover of fire resistant PFTs (high R). In other
385 words, plants having a strong fire response could effectively maintain a high cover for any
386 flammability and fire frequency; while plants having a weak fire response displayed a lower
387 flammability that led to infrequent fires, thus allowing for the plant spread and resulting in high
388 plant cover values. Furthermore, the response-flammability relationship was stronger for slow than
389 for fast colonizer plants: given a (R, L) pair value, the average vegetation cover depended on the
390 time scale of plant colonization. Faster colonizing PFTs had a greater cover (Fig. 1C) than slower

391 ones (Figure 1D), despite the higher fire frequency associated with the former (Figure 1A)
 392 compared to the latter (Fig. 1B).

393



394

395

396 *Figure 1. (A-B) Average fire return time ($\langle T \rangle$, color scale) and (C-D) average vegetation cover ($\langle b \rangle$,*
 397 *color scale) in the parameter plane of fire response (R , x-axes) and flammability (L , y-axes). (A-C) fast*
 398 *colonizer: $c=0.3 \text{ yr}^{-1}$ and $m=0.03 \text{ yr}^{-1}$. (B-D) slow colonizer: $c=0.05 \text{ yr}^{-1}$ and $m=0.005 \text{ yr}^{-1}$. The average*
 399 *values were computed over 50 realizations. The maximum value of $\langle b \rangle$ in the absence of fire is $\langle b \rangle = 1 -$*
 400 *m/c , which provides a value of 0.9 (Tilman, 1994) for both panels C and D, and across the whole*
 401 *parameter plane (R, L). The scale of the fire return time $\langle T \rangle$ was arbitrarily cut at 100 yr for clarity of*
 402 *representation, yet values ranging up to 10,000 yr were observed at low L values.*

403

404 The effect of the plant colonization parameter (related to the time scale of plant growth) can be
 405 explained by using the non-dimensional formulation of our model (Eq. A2-A4 in Appendix A). If
 406 the rescaling of the non-dimensional model is applied to Fig. 1, i.e. using the non-dimensional

407 flammability L/c as a vertical axis and representing the rescaled vegetation cover $\frac{b}{\left(\frac{c-m}{c}\right)}$, then Fig.
408 1C becomes the same as Fig. 1D. This is shown in Fig. A1 (Appendix A), for a set of non-
409 dimensional flammability values and different combinations of R , L , c and m .

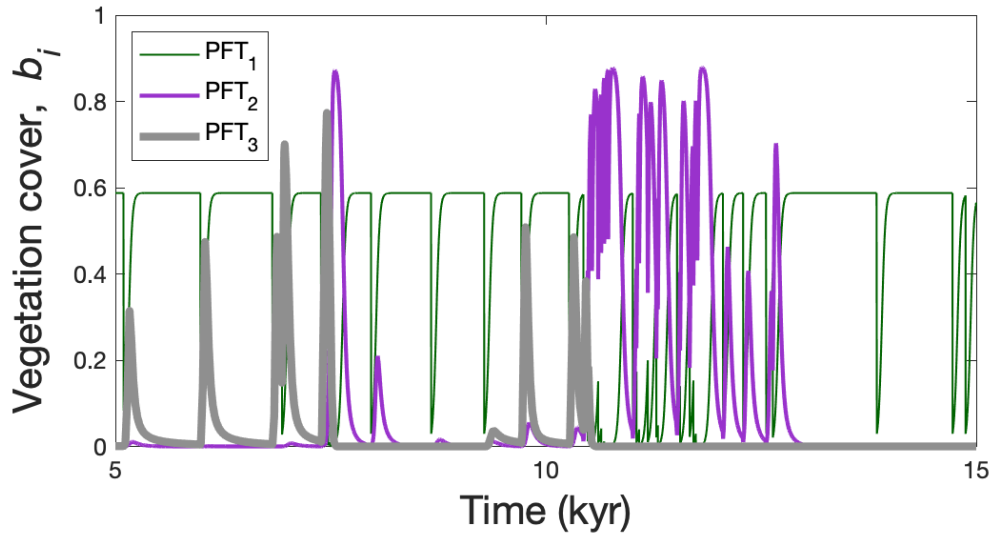
410

411 *3.2 Community emergence*

412 In the absence of fire, a closed canopy forest of the late successional PFT₁ tree established in all
413 the three case studies, i.e. for the reference parameter values reported in Table 2. When including
414 fires, only the Mediterranean case study preserved this stable state, while the tropical and boreal
415 cases showed alternative ecological states (Figure 2-4). In particular, in the Mediterranean
416 community, the evergreen, fire-resistant oak (PFT₁) eventually outcompeted the other PFTs by
417 maintaining a long fire return time (Fig. C2A in the Appendix) that averaged to 490 yr (in line
418 with Baudena et al. 2020; Vasques et al. 2022). For the tropical communities, depending on the
419 initial condition and on the specific stochastic fire sequence, we observed the establishment and
420 maintenance of either a closed canopy forest (PFT₁) or a mix of savanna trees and grasses
421 (PFT₂+PFT₃). These alternative states respectively corresponded to average fire return times of
422 1045 yr and 4 yr (Fig. C3A in the Appendix), in line with observations (e.g., D’Onofrio et al.
423 2018). Such a result was expected as humid savannas and tropical forests are observed in areas
424 with the same environmental conditions but different fire frequencies (Hirota et al. 2011; Staver
425 et al. 2011b; Dantas et al. 2016), which is commonly explained as an indication of alternative
426 biome states maintained by a fire-vegetation feedback (e.g., Accatino et al. 2010; Staver and Levin
427 2012). In the boreal case study, fires triggered the irregular alternation between forests of either
428 embracer conifers (PFT₂), avoider conifers (PFT₁), or a mixedwood forest including deciduous
429 trees and late successional evergreen conifers (PFT₁+PFT₃). This alternation persisted through the
430 whole time series, see Figure 2, creating recurrent but irregular sequences of states. Mosaics of
431 different plant communities are commonly observed in boreal North America landscapes
432 (Bormann and Likens 1979; Baker 1989; Gummer et al. 1996; Johnson et al. 1998; Weir et al.
433 2000). According to our simulations, the mosaic would be generated by the combination of: i) the
434 irregular alternation between communities sustained by different fire frequencies within each patch
435 (more frequent fires in embracer conifer forests, with 80 yr average fire return time, and less
436 frequent fires in mixedwood or late successional conifer forests, with respectively about 100 and

437 450 yr average fire return time), and ii) asynchrony in fire dynamics (matching differing and
 438 independent fire histories) between patches of the same landscape. This asynchrony is similar to
 439 the gap dynamics observed by Wissel (1992). In addition, the communities reported here are in
 440 line with field observations of most common communities (Jasinski and Payette 2005; Couillard
 441 et al. 2012) and paleoecological findings, which identify recurrent turnovers between balsam fir
 442 and black spruce communities, characterized by fire frequency shifts (Ali et al. 2008; de Lafontaine
 443 and Payette 2010; Couillard et al. 2018).

444



445

446 *Figure 2. Example of a time series of fractional vegetation cover (avoider conifer PFT₁: green thin line;*
 447 *embracer conifer PFT₂: purple line; deciduous trees PFT₃: gray thick line) observed in the model for the*
 448 *North American boreal communities (parameter values as in Tab. 2).*

449

450 3.2.1 Main characteristics shaping plant communities

451 The parameter sensitivity analysis (RQ2) showed that a few key plant characteristics, depending
 452 on the biome, influenced the emergence of different communities in this model (Fig. 3 and Sec.
 453 2.3.2). Such emergence depended on the ability of a PFT to persist given the constraints imposed
 454 by the other plants, in terms of competition for resources and fire frequency.

455

456 In the Mediterranean case study (left panels in Fig.3), a state change was observed only for low
 457 fire response values of the strongest competitor PFT₁ (R_I), where the PFT₁ forest became bistable

458 with a shrubland, PFT₃. Conversely, for medium-to-high values of R_I or for changes in all other
459 parameters, the PFT₁ forest was the only observed state.

460

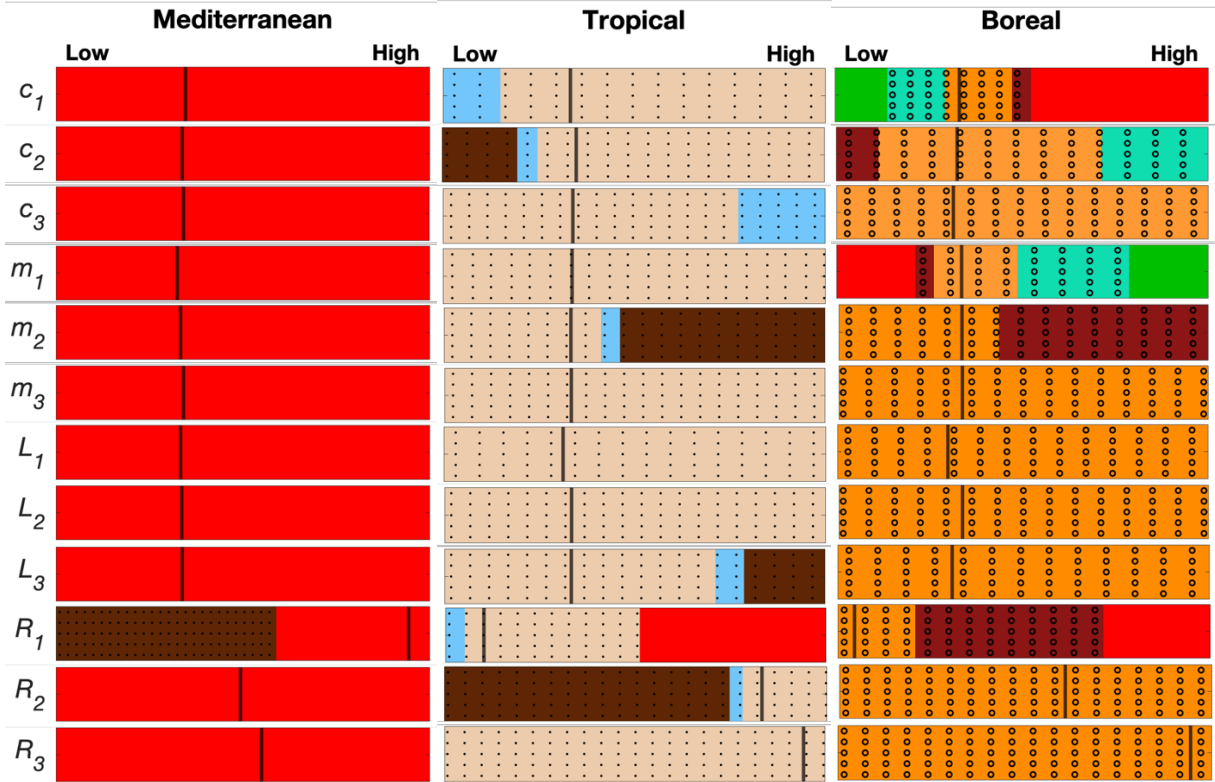
461 In the tropical (central panels in Fig. 3) and boreal (right panels of Fig. 3) case studies, the picture
462 was more complex. State changes were observed for variations in the colonization rate of nearly
463 all PFTs, except for PFT₃ in the boreal case. On the other hand, modifying the mortality rates led
464 to fewer state changes (i.e., m_2 in the tropical case and both m_1 and m_2 in the boreal case). For each
465 of the PFTs, a c_i - m_i relationship emerged in the model: the ecological states observed when
466 increasing the colonization rates with respect to the reference values (black vertical lines in Fig. 3)
467 were similar to the ones observed when decreasing the mortality rate, and vice versa (see Fig. D1
468 in the Appendix). Yet, the colonization rate led to the highest number of overall state changes. No
469 changes were observed in the explored L_1 and L_2 ranges, while only large values of L_3 in the
470 tropical communities led to state changes. Concerning the fire responses, a PFT₁ forest was always
471 present at large R_I , while bistable states (PFT₁/PFT₂+PFT₃ for the tropical community) or temporal
472 alternation between states (PFT₁/PFT₂/PFT₁+PFT₃ for the boreal community) appeared at low R_I ,
473 in analogy with the Mediterranean case. State changes emerged at low values of R_2 for the tropical
474 case only, while no state change was observed in the whole R_3 range.

475

476 In conclusion, the parameters that mostly changed the long-term ecological state across the three
477 communities were: R_I , c_1 and c_2 .

478

479



480

481 *Figure 3. Community state maps (see color legend) observed for individual parameter variations, for the*
 482 *Mediterranean (left), tropical (center) and boreal (right) communities. Black vertical lines represent the*
 483 *reference values in Tab. 2. Parameters were individually changed from 0.5 (Low) to 2 (High) times their*
 484 *reference value, except for fire responses (R_i) that were changed between 0.01 (Low) and 0.9 (High).*

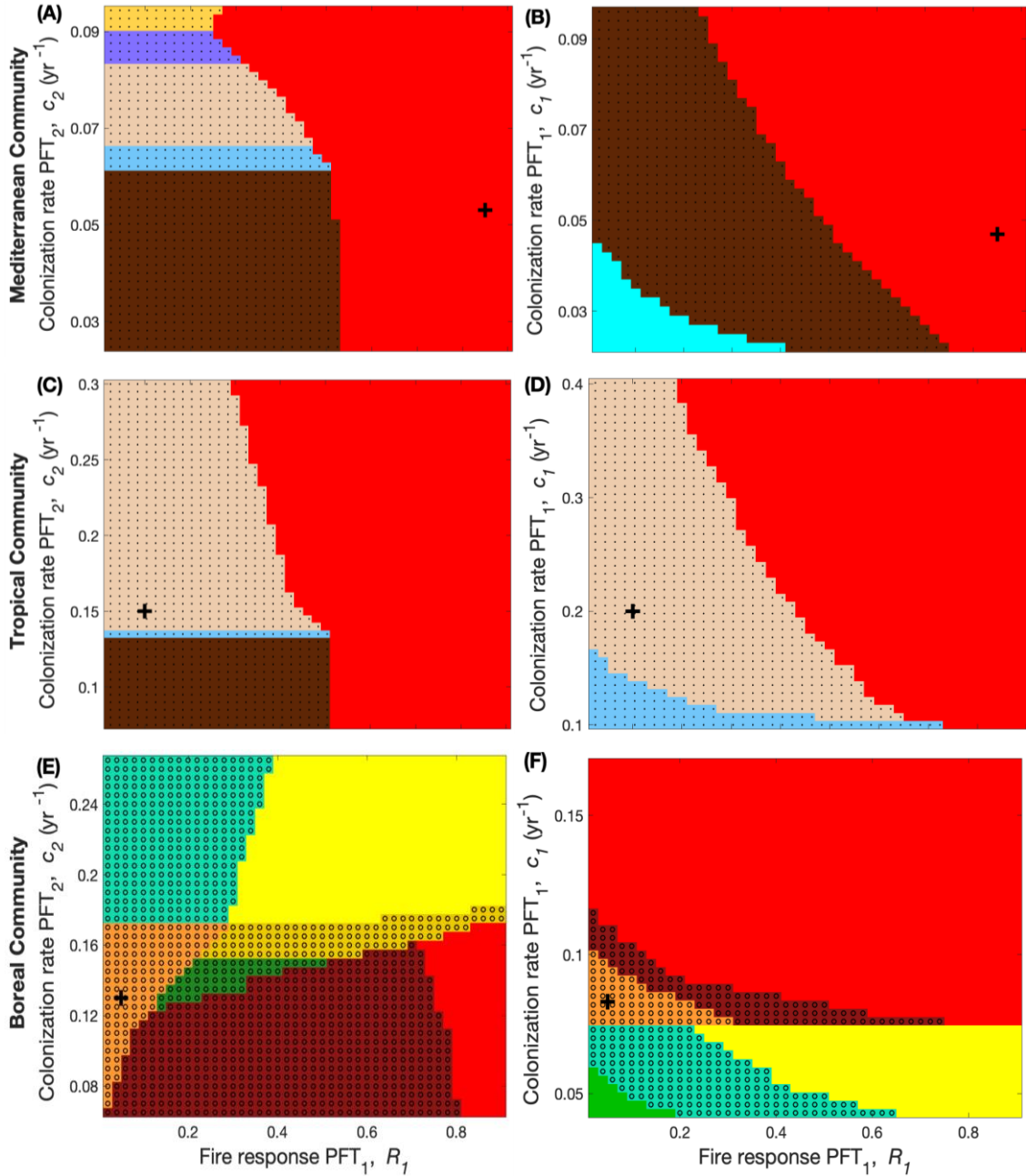
485

486 3.2.2 Combinations of plant characteristics leading to alternative ecological states

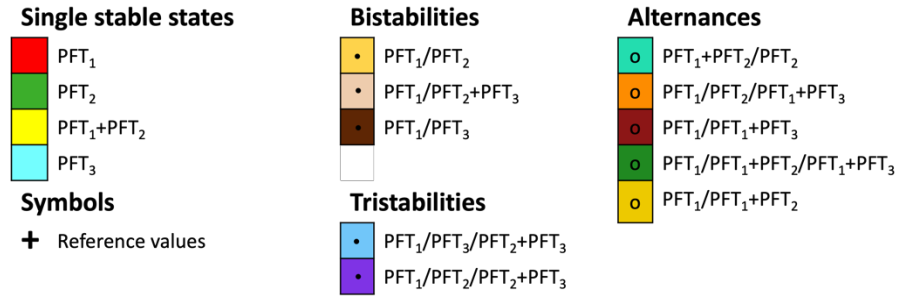
487 To answer RQ3, we explored three plane sections in parameter space, each defined by pairs of the
 488 three parameters selected in Sec 3.2.1 (i.e. R_i , c_1 and c_2). Among those, we observed few state
 489 changes when expanding around the reference values of the PFT₁ and PFT₂ colonization rates, i.e.
 490 the c_1 - c_2 plane shown in Fig D2 in the Appendix. As expected from the earlier analysis (Fig. 3), a
 491 PFT₁ forest was the only state observed in the whole c_1 - c_2 plane (Fig. D2-A) for the Mediterranean

492 case. In the tropical (Fig. D2 B) and boreal (Fig. D2C) cases, stable states emerged at either high
 493 or low values of PFT_1 colonization rate, while bistable states or irregular alternance of states
 494 respectively emerged for the two cases at intermediate values of c_1 . Since the Mediterranean case
 495 suggested a decisive effect of the fire response of the strongest competitor, R_1 , on the stability of
 496 the observed communities, we further focused the analysis on the R_1 - c_2 and R_1 - c_1 planes (Fig. 4).

497



499



500

501 *Figure 4. Community state maps (see color legend) observed in the parameter plane of the fire response*
 502 *of PFT₁, R₁ (x-axis) in combination with either the colonization rate of PFT₂, c₂ (A, C, E) or the*
 503 *colonization rate of PFT₁, c₁ (B, D, F) for (A-B) Mediterranean, (C-D) humid tropical and (E-F) Boreal*
 504 *communities. The parameter reference values (Tab. 2) are identified by the black crosses.*

505

506 *The fire response of PFT₁ (R₁) and the colonization rate of PFT₂ (c₂)*

507 In the Mediterranean biome, when exploring the R₁-c₂ plane (Fig. 4A), the dominance of PFT₁ was
 508 maintained at large R₁ values for any value of c₂. At low R₁ values, the PFT₁ forest became bistable
 509 with other states, whose specific composition depended on the PFT₂ colonization rate. There, the
 510 weak fire response of PFT₁ and its slow colonization time scale compared to the other PFTs made
 511 it susceptible to die out under high fire frequency. Across the time series, if the cover of the other,
 512 more flammable, plants became large enough to maintain a short fire return time, PFT₁ would
 513 succumb. If, otherwise, PFT₁ dominated the community, a low fire frequency was maintained,
 514 allowing this late successional plant to outcompete the others during the fire-free periods. When
 515 bistability was possible, we observed that whether the system ended up in one or the other state
 516 depended on the initial plant cover of the community and on the specific sequence of stochastic
 517 fires that might lead to a series of short or long fire intervals (see also Appendix C). Similar
 518 dynamics drove the occurrence of alternative ecological states also in the other case studies. Tri-
 519 stability was observed at the borders between areas of different types of bistability.

520

521 The bistability between tropical forest and savanna was observed in a broad part of the R₁-c₂ plane
 522 (Fig. 4C), where the fire response of PFT₁ was low. Remarkably, the pattern of states in the tropical
 523 parameter space was not dissimilar from the Mediterranean case (compare Fig. 4C with Fig. 4A):
 524 a broad area of PFT₁ dominance was observed at large R₁, bistable states were possible at
 525 intermediate to low R₁, and regions of tri-stability occurred at the edges between these areas of

526 bistability. This similarity of behavior was interesting, as the characteristics of the Mediterranean
527 PFTs were substantially different from the corresponding tropical PFTs. The latter displayed faster
528 dynamics (given by c_i and m_i), stronger fire response of PFT₂, and higher flammability of PFT₂
529 and PFT₃.

530

531 In the boreal biome, the irregular alternation of forests of either late successional conifers (PFT₁),
532 embracer conifers (PFT₂), or a mixedwood forest (PFT₁+PFT₃) was observed in a narrow region
533 of the parameter plane, at low R_I values. In analogy with the other case studies, the temporal
534 alternation of different communities was observed at intermediate to low R_I , while stable
535 ecological states were observed at high R_I values (Fig. 4E). These stable states corresponded to
536 either a PFT₁ forest, at low colonization rate of PFT₂, or to a PFT₁+PFT₂ forest, at high colonization
537 rate of PFT₂. The existence of two stable states at large R_I differed from the other case studies, and
538 it follows from Tilman's (1994) model. In the absence of fire, PFT₂ can coexist with PFT₁ when
539 its colonization rate is fast enough to compensate for losses due to competition pressure, i.e. $c_2 >$
540 $\frac{c_1(c_1 - m_1 + m_2)}{m_1}$. Using the reference values for c_1 , m_1 and m_2 (Tab. 2), this condition corresponds to
541 $c_2 > 0.158 \text{ yr}^{-1}$ in the boreal case, which closely corresponds to the value of c_2 that separates the
542 PFT₁ and PFT₁+PFT₂ states at large R_I in Fig. 4E.

543

544 For all three case studies, the ecological states observed at large R_I values were the same as those
545 predicted by Tilman's unperturbed model for the c_i and m_i values used in that region of parameter
546 space. This corresponded to a stable PFT₁ state for both the Mediterranean and tropical cases,
547 where Tilman's coexistence condition is never satisfied in the explored range of c_2 parameter
548 values. In contrast, Tilman's coexistence condition is met in part of the explored range of Fig. 4E,
549 and both PFT₁ and PFT₁+PFT₂ states are observed at large R_I values. Consequently, the
550 competition between PFTs mostly drove the community dynamics at large R_I values.

551

552 *The fire response of PFT₁ (R_I) and the colonization rate of PFT₁ (c_1)*

553 We observed a relationship between the colonization rate and the fire response of PFT₁ (Fig 4B,
554 D, F). As c_1 values increased, the stable state region characterized by PFT₁ alone (in the
555 Mediterranean, boreal and tropical communities) or PFT₁ coexisting with PFT₂ (in the boreal

556 community) became wider, progressively extending towards low R_I values. Hence, in order to
557 maintain a stable fire community, PFT₁ needs to be either very fire resistant (large R_I) or very fast
558 in its colonization rate (large c_1), as this also ensures rapid expansion after fire. Conversely, a fire
559 intolerant PFT₁ could be lost from the community if its colonization ability was insufficient,
560 despite its superior competitive ability. This was, for instance, observed at low R_I and low c_1 values
561 in the Mediterranean and boreal communities, where respectively stable states of PFT₃ and PFT₂
562 emerged. In the boreal case (Fig. 4F), we also observed a sharp transition at about $c_I=0.07\text{yr}^{-1}$,
563 that identified a state change between PFT₁ and PFT₁+PFT₂ forests at large R_I . This again matched
564 Tilman's coexistence condition (Tilman, 1994) for the no-fire dynamics, as recalled above, i.e. c_I
565 $< 0.078 \text{ yr}^{-1}$ using the reference values of c_2 , m_2 and m_1 (Tab. 2).

566
567 The relationship between the PFT₁ colonization rate and its fire response was confirmed for
568 concomitant variations of the PFT₁ and PFT₂ colonization rates. In a version of the R_I - c_2 parameter
569 plane simulated for a lower value of c_1 , the colonization rate of the strongest competitor PFT₁
570 (Figure D3 in the Appendix), the patterns of states described above (Figure 4 A,C,E) seemingly
571 shifted towards higher values of PFT₁ fire response for all the biomes (thus towards the right in
572 the figures). At low fire response values, new (mostly stable) ecological states emerged.

573
574 Finally, the inclusion of seed spreading from the surrounding environment originated irregular
575 alternation among the ecological states in the Mediterranean and tropical cases. However, this
576 hardly affected the ecological patterns shown in Fig. 4. In particular, the communities involved in
577 the multiple ecological states of Fig. 4 could alternate across the time series (similar to that
578 observed in the boreal case and in Casagrandi and Rinaldi 1999), while regions of parameter space
579 where only one ecological state was possible were not affected by the inclusion of the seed inflow
580 from neighboring areas.

581

582 **4 Discussion**

583 In the model presented here, the fire response emerged as a key plant characteristic influencing
584 PFT density, fire frequency and the existence of one or more communities in different fire biomes.
585 For single PFTs (RQ1), less flammable plants can have a high cover over a wide range of fire

586 responses, while highly flammable plants have to display a strong fire response to maintain a high
587 cover. In a competitive fire-prone community, the fire response of the strongest competitor
588 determined whether only one or multiple alternative ecological states were feasible (RQ3): a strong
589 fire response resulted in the existence of only one stable state, whereas a weak fire response
590 allowed for the existence of alternative ecological states. In the latter case, the colonization rate of
591 both the strongest competitor and the second-best competitor explained the observed communities
592 in different fire prone ecosystems (RQ2).

593

594 In the absence of competition from other plants, the vegetation cover and the fire frequency of a
595 single standing PFTs shaped each other via the fire-vegetation feedback. A relationship between
596 the fire response of a single PFT and its flammability spontaneously emerged in our model, and
597 this relationship was mediated by the PFT colonization time scale (similar to Jaureguiberry and
598 Díaz 2023). In detail, less flammable plants generally led to rare fires and maintained a large cover
599 over a broad range of fire responses. Conversely, highly flammable plants, leading to frequent
600 fires, can maintain a high cover if they are slow growers and fire tolerant (high values of parameter
601 R), while they can display an intermediate to strong fire response if they are fast colonizers. The
602 plant colonization rate, together with the fire response, determined the average fire frequency and
603 plant cover: PFTs that spread rapidly were also fast at recovering after fires, even when the fire
604 response of the plants was weak, thus ensuring high plant cover (Eq. 4).

605

606 Real plant behavior supports the model results. According to ecological observations, resprouting
607 species are indeed present in ecosystems having various fire frequencies, spanning from the
608 flammable eucalyptus forests in Australia (STRASSER et al. 1996) to the less flammable oak
609 forests in the Mediterranean basin (see e.g., references in Table 2); although, resprouting attributes
610 are more common in ecosystems where the fire frequency is higher, especially for woody plants
611 (Harrison et al. 2021). Conversely, fire intolerant trees, such as tropical forest trees, generally
612 create a moist understory and therefore decrease ecosystem flammability. Once infrequent fires
613 allow the establishment of those trees, they maintain a low ecosystem flammability that creates a
614 positive feedback, further allowing their spread. On the other hand, in fire-prone environments,
615 fast colonizers, such as grasses or early successional shrubs, are often highly flammable, although
616 their fire response can span from the highly fire-adapted savanna and Mediterranean grasses (see

617 e.g., Baudena et al. 2020) that can resprout, to the weak fire response of some annual grasses, such
618 as cheatgrass (*Bromum tectorum*; Zouhar 2003). This latter grass is infamous for its success in
619 invading North American prairies and changing their fire regime (Fusco et al. 2019), yet it does
620 not resprout and has seeds that are susceptible to heat kill (but can survive underground when
621 already present). The fast colonization rate of field layer species guarantees their survival
622 independently of their fire response, as long as some individuals and propagules are not totally
623 burned. Our findings indicate that these types of behavior might be due to fires acting as a filter
624 on species characteristics and their possible associations. This agrees with evolutionary theories
625 and modeling outcomes suggesting that flammability, despite its negative effects on individuals,
626 may have evolved in combination with other advantages, such as higher recruitment opportunities
627 or resprouting (Bond and Midgley 1995; Schwilk and Kerr 2002). It should be noted that, despite
628 the similarities between the trait syndromes found in this work and in evolutionary studies, in our
629 model we cannot establish a causal relationship between these characteristics.

630

631 Within the framework of the model, plant survival in a community was further constrained by the
632 features of other species adapted to the same environment. In particular, the characteristics of the
633 most competitive PFT were found to be of primary importance for community composition in the
634 long term (Figure 2). When the strongest competitor also had a strong fire response, only one type
635 of community was possible: a forest of this late successional tree (in the Mediterranean and tropical
636 case study), which could coexist with the embracer conifer in the boreal case study. Conversely,
637 when the strongest competitor had weak to intermediate fire response, two or more alternative
638 ecological states were possible (Figure 2), and the specific composition of the observed
639 communities mostly depended on the colonization rates of the two best competitors. Here, we also
640 note that the colonization rates of the two best competitors (together with their mortality rates)
641 determined the competition strength of the first on the latter (i.e., of PFT₁ on PFT₂), as shown by
642 the derivation of the non-dimensional model (Eq. A6 in Appendix A). The combination of the fire
643 response of the strongest competitor and the competition strength between the two best competitors
644 explained the presence of a stable forest of resprouter holm oak in the Mediterranean basin (Amici
645 et al. 2013; Carnicer et al. 2014), the bistability between the fire-intolerant tropical forest and
646 humid savannas (Staver et al. 2011a; Dantas et al. 2016; D'Onofrio et al. 2018) and the temporal
647 alternation of fir- or spruce-dominated forests reported for North America by palaeoecological

648 records (Couillard et al. 2018). Moreover, the drivers that we identified for the plant communities
649 agree with, and expand on those used by Van Nes et al. (2018), which explain the forest-savanna
650 bistability as a tradeoff between growth and fire-induced mortality of trees.

651
652 The factors that mostly decide the community composition in this model closely correspond to the
653 classification of plant persistence conditions proposed by Pausas and Lavorel (2003). This
654 framework suggests that, in a fire prone and competitive community, plant attributes determine
655 the possibility of plant persistence at either individual, population, community or landscape level.
656 While our model did not have explicit representation of these persistence levels, and therefore PFT_i
657 persistence corresponds only to a positive fractional cover ($b_i \neq 0$), we can connect persistence
658 levels to model parameters. Persistence of individuals after fire (e.g., due to resprouting) was
659 represented by large values of the fire response parameter, while population persistence (e.g. due
660 to a fire-resistant seed-bank) corresponded to intermediate-to-low fire response values. In the
661 model, the fire response of the strongest competitor was also a key factor in determining the
662 ecological states. The persistence condition at community level, i.e. species survival in a
663 competitive environment between fire events, is due to competitive ability in Pausas and Lavorel's
664 framework. Analogously, in our model, the competition strength between the two best competitors
665 (determined by the colonization and mortality rates of PFT_1 and PFT_2 , see Eq. A6 in appendix A)
666 is crucial for determining the community composition. Finally, the framework predicted that the
667 explicit representation of external seed dispersal might lead to species persistence at landscape
668 level. In our model, seed dispersal could lead to temporal alternation between states, but had the
669 weakest effect on the community composition. This correspondence with the early conceptual
670 work of Pausas and Lavorel (2003) brings ecological support to our results. Furthermore, since the
671 importance of these persistence levels emerged from the dynamics of the model rather than being
672 strictly imposed, our results provide quantitative support to such a theoretical ecological
673 framework. In addition, we showed that different persistence strategies could be related, such as
674 the individual/population (R_i) and community (c_i) persistence levels (Figure 4B, D, F): the
675 competition strength depended on the colonization rate of the PFTs, which in turn regulated the
676 regrowth time between consecutive fires, thus having a complementary role with the fire response
677 of a certain PFT.

678

679 Sequences of long (or short) fire return times, which randomly occurred in the fire series, often
680 started the exclusion of PFTs and the transition between different communities (see Appendix C).
681 These sequences triggered the fire-vegetation feedback, which resulted in the state change. For
682 stable or bistable communities, as in the Mediterranean and Tropical cases, such sequences played
683 an important role in the initial part of the simulations, when they allowed a community to become
684 dominant. At that point, the established community was maintained in time by the fire-vegetation
685 feedback, while the PFTs not included in the community eventually died out. This agreed with
686 observations suggesting that accidentally frequent (or infrequent) fires can prevent (or foster)
687 transitions between stages of tropical forest development (Lehmann et al. 2011; Hoffmann et al.
688 2012; de L. Dantas et al. 2013). In the case of irregular alternances, the transitions between states
689 occurred across the whole simulation time, as can be seen in Fig. 2 (e.g. between 10 kyr and 13
690 kyr). In this case, all the PFT covers were positive along the whole simulation time, despite
691 sometimes reaching very low values ($b \approx 0.001$). Hence, specific sequences of short or long fire
692 return time allowed the blowing up of one or more of the PFTs and caused a (temporary) state
693 change. The same mechanism triggered alternation between states when including seed dispersal.
694 Because an increasing frequency of extreme events is expected according to climate change
695 projections (Keeley and Syphard 2019; Masson-Delmotte et al. 2021), it becomes important to
696 include stochastic effects for studies on possible state transitions in fire-prone communities.

697
698 Although the model does not explicitly include climate factors, regional climate gradients or
699 climate change are expected to modify plant behavior, as represented by the model parameter
700 values. Hence, we can use the results of the sensitivity analysis to speculate on the possible changes
701 of fire-prone ecosystems in response to climate variations. For instance, black spruce (PFT₂)
702 dominates in the western part of North America, where the climate is drier than in the eastern area,
703 resulting in the slowing down of balsam fir (PFT₁) establishment and growth (Frank 1990;
704 Goldblum and Rigg 2005). This would correspond to the reduction of the PFT₁ colonization
705 parameter (c_1) in the model, i.e. downward migration of the black cross in Fig. 4F, which explains
706 the loss of PFT₁ (balsam fir) and the dominance of PFT₂ (black spruce) observed in the western
707 boreal North American regions. Similar exercises may give indications on possible community
708 changes under climate change scenarios. Global warming, changes in precipitation regimes and a
709 general tendency towards increasing aridity and drought occurrence are predicted over large

710 portions of the planet (Masson-Delmotte et al. 2021), which will affect plants, fires and their
711 interactions (Bradstock 2010; Higgins and Scheiter 2012). As a rule of thumb, the predicted
712 changes are expected to slow down plant colonization rates, increase plant flammability and
713 possibly reduce plant fire response, thus shifting the modeled systems towards the bottom left
714 corner in Fig. 4. This would for instance lead the Mediterranean oak forest to become bistable with
715 an open shrubland (Fig 4A-B) and even disappear completely under the most extreme reductions
716 (Fig. 4B and Fig. D3A in the Appendix), in line with previous findings (Batllori et al. 2019;
717 Baudena et al. 2020).

718
719 This model is expected to be adaptable to any fire ecosystem worldwide. Clearly, it is also a
720 simplified representation of real ecosystems. For example, fire response may not be constant in
721 time: some seeders, such as pines in the Mediterranean Basin (Pausas 1999a; Climent et al. 2008),
722 only produce seeds when mature, resulting in a demographic bottleneck if a second fire occurs
723 before maturity is reached. Likewise, no intraspecific dynamics are accounted for, and spatial
724 processes are not represented, while spatial vegetation patterns might prevent the occurrence of
725 alternative ecosystem states (Rietkerk et al. 2021). Despite these simplifications, our results agree
726 with the findings of models that explicitly represent seedbank dynamics (Baudena et al. 2020) (or
727 spatial processes (Vasques et al. 2022)). In addition, the limited number of parameters make this
728 model an efficient conceptual framework, which can also be examined analytically in some cases
729 (Baudena et al. 2020).

730 Despite the variety of models accounting for fire dynamics (Williams and Abatzoglou 2016), the
731 degree of complexity that is required to capture the main features of fire-prone ecosystems is still
732 unclear. In this context, our study underlines the importance of representing plant fire response.
733 An improved representation of plant post-fire recovery led to a better reproduction of the forest
734 burned area observed in western US (Abatzoglou et al. 2021). The representation of plant fire
735 strategies improved simulations of fire regimes in Australian savannas using LPX (Kelley et al.
736 2014), a Dynamic Global Vegetation Models (DGVMs, e.g., Prentice et al. 2007). More generally,
737 DGVMs often account for only a hurried conceptualization of post-fire recovery, and do not
738 include resprouting as a trait (Kelley et al. 2014; Hantson et al. 2016; Venevsky et al. 2019;
739 Harrison et al. 2021). We envisage that an improved representation of fire response could reduce

740 projection uncertainties and assist also in ecosystem management and landscape planning for fire
741 prevention (Hantson et al. 2016).

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1313

1314 **List of tables**

1315 Table 1 (2 pages)

1316

Biomes and location	Mediterranean forest and scrubs (Mediterranean basin)	
PFT identification	PFT₁ : <i>Quercus ilex</i>	PFT₂ : <i>Pinus</i> spp. PFT₃ : <i>Rosmarinus officinalis</i> , <i>Cistus</i> spp., <i>Ulex</i> spp
Shade tolerance	High : late-successional, broad-leaved evergreen	Medium : outcompeted by <i>Quercus ilex</i> (in mesic conditions) Low : shrubs and perennial grasses outcompeted by trees
Fire response	Strong : high individual fire resistance, resprouts readily after fires	Intermediate : resistance at population level, post-fire seed release, serotinous cones in some species, thin juvenile bark, cones destroyed by severe crown fires, seedbank not produced in case of frequent fires preventing pines to reach maturity Intermediate : shrubs: seeders with large seed banks and gradual seedbank decay, affected by ground fires; <i>B. retusum</i> : resprouter grass
Flammability	Low : moist and cool understory, very little fine and dead standing fuel, infrequent fires, average fire return time of 500 yr	High : average fire return time of ~10yr
References	(Acácio et al. 2007; Puerta-Pinero et al. 2007; Saura-Mas et al. 2009; Timmer et al. 2009; Baeza et al. 2011; Amici et al. 2013; Azevedo et al. 2013; Clarke et al. 2013; Zeppel et al. 2015; Vayreda et al. 2016; Baudena et al. 2020) (Pausas 1999a, 1999b; Zavala et al. 2000; Zavala and Zea 2004; Rodrigo et al. 2007; Climent et al. 2008; Fernandes et al. 2008; Karavani et al. 2018) (Hanes 1971; Baeza et al. 2006; Acácio et al. 2009; Santana et al. 2010; Acácio and Holmgren 2014)	

Biomes and location	Tropical savanna and forest			Boreal forest (North America)		
PFT identification	PFT₁ : Forest trees	PFT₂ : Savanna trees	PFT₃ : C4 grasses	PFT₁ : <i>Abies balsamea</i> , <i>Picea glauca</i>	PFT₂ : <i>Picea mariana</i> , <i>Pinus Banksiana</i>	PFT₃ : <i>Betula papyrifera</i> , <i>Populus tremuloides</i>
Shade tolerance	High : broad leaved	Medium-Low : juvenile light sensitivity	Low : grows in canopy gaps or coexists with trees having low brunch density (e.g. savanna trees)	High : late successional trees	Intermediate : replaced by late successional species	Low : pioneer species, rare in late successional communities, can grow in forest canopy gaps
Fire response	Weak : low resistance at PFT level, fire-sensitive trunk	Strong : resistance at individual level, thick bark, survive to frequent ground fires	Strong : resistance at individual level, strong resprouters	Weak : low resistance at PFT level, avoider, seeder, seeds often destroyed by fires, survival trough unburned adult trees	Intermediate : high resistance at PFT level, embracer, semi-serotinous cones	Strong : high resistance at individual level, resister, resprouts form root collar when killed by fires
Flammability	Low : humid and shady understory, infrequent fires, average fire return time of ~1000yr	High : frequent fires, average fire return time of 3-5yr	High : fast-spreading ground fires occurring possibly every year	Low : fires almost absent in <i>Abies b.</i> forests, average fire return time of 250-300yr	Intermediate : layered structure, resinous wood, average fire return time of ~75yr	Low : high canopy moisture content, infrequent fires, average fire return time ~100yr
References	(San José and Farinas 1991; Kurokawa et al. 2003; Laurance et al. 2004; Russell-Smith et al. 2004; Bampfylde et al. 2005; Rossatto et al. 2009; Geiger et al. 2011; Viani et al. 2012; de L. Dantas et al. 2013; D'Onofrio et al. 2018)	(Beckage et al. 2009; Warman and Moles 2009; Accatino et al. 2010; Lehmann et al. 2011; Hoffmann et al. 2012; de L. Dantas et al. 2013)	(Accatino et al. 2010; Baudena et al. 2010)	(Rowe and Scotter 1973; (Viereck 1983; Payette 1992; Uchytill 1991a; Galipeau Carey 1993; Larsen 1997; et al. 1997; Sirois 1997; Greene and Johnson 1999; Bergeron 2000; Ali et al. 2000; Amiro et al. 2001; Wirth 2005; Ali et al. 2008; de Lafontaine and 2008; Bouchard et al. 2008; de Lafontaine and Payette 2010; Couillard et al. 2012; Johnstone et al. 2010, 2020; Payette et al. 2012; Fryer 2014; Abrahamson 2014; Rogers et al. 2015)	(Rowe and Scotter 1973; (Viereck 1983; Payette 1992; Uchytill 1991a; Galipeau Carey 1993; Larsen 1997; et al. 1997; Sirois 1997; Greene and Johnson 1999; Bergeron 2000; Amiro et al. 2000; Amiro et al. 2001; Wirth 2005; Ali et al. 2008; de Lafontaine and 2008; Bouchard et al. 2008; de Lafontaine and Payette 2010; Couillard et al. 2012; Johnstone et al. 2010, 2020; Payette et al. 2012; Fryer 2014; Héon et al. 2014; Rogers et al. 2015; Couillard et al. 2018; Hart et al. 2019, 2019)	(Swain 1980; Uchytill 1991b; Zasada 1992; Payette 1993; Howard 1996; Larsen 1999; Greene and Johnson 1999; Bergeron 2000; Brassard and Chen 2006; Bouchard et al. 2008; Bergeron and Fenton 2012; Rogers et al. 2013; Hart et al. 2019; Mack et al. 2021)

1319 Table 2
 1320

Parameter	Mediterranean	Tropics	Boreal	Units
c_1	0.047	0.20 (>0.15-2.50)	0.085	yr ⁻¹
c_2	0.053	0.15 (0.15-2.50)	0.13	
c_3	0.3	20 (20-200)	0.17	
m_1	0.0025	0.01	0.035	yr ⁻¹
m_2	0.008	0.06 (0.03-0.3)	0.015	
m_3	0.03	3 (1-3)	0.023	
L_1	1/500	1/1000	1/250	yr ⁻¹
L_2	1/20	1/5	1/75	
L_3	1/10	1/2 (1/2-1)	1/100	
R_1	0.85 (0.80-0.90)	0.10 (0.10-0.30)	0.05 (0.05-0.20)	-
R_2	0.40 (0.30-0.50)	0.70 (0.60-0.80)	0.55 (0.4-0.6)	
R_3	0.50 (0.40-0.60)	0.85 (0.75-0.95)	0.85 (0.8-0.9)	

1321
 1322

1323 List of legends

1324 **Table 1.** Characteristics of each PFT in the three case studies: Mediterranean, Tropical and Boreal North
 1325 America biomes.

1326
 1327 **Table 2.** Reference parameter values of colonization rate (c_i), mortality rate (m_i), flammability (L_i) and
 1328 fire response (R_i) of PFT_{1,2,3} as parameterized for Mediterranean, tropical and boreal communities.
 1329 Possible ranges identified in the parameterization (Appendix B) are reported in parentheses.

1330
 1331 **Figure 1.** (A-B) Average fire return time ($\langle T \rangle$, color scale) and (C-D) average vegetation cover ($\langle b \rangle$,
 1332 color scale) in the parameter plane of fire response (R , x-axes) and flammability (L , y-axes). (A-C) fast
 1333 colonizer: $c=0.3$ yr⁻¹ and $m=0.03$ yr⁻¹. (B-D) slow colonizer: $c=0.05$ yr⁻¹ and $m=0.005$ yr⁻¹. The average
 1334 values were computed over 50 realizations. The maximum value of $\langle b \rangle$ in the absence of fire is $\langle b \rangle=1$ -

1335 m/c, which provides a value of 0.9 (Tilman, 1994) for both panels C and D, and across the whole
1336 parameter plane (R,L). The scale of the fire return time $\langle T \rangle$ was arbitrarily cut at 100 yr for clarity of
1337 representation, yet values ranging up to 10,000 yr were observed at low L values.

1338

1339 **Figure 2.** Example of a time series of fractional vegetation cover (avoider conifer PFT₁: green thin line;
1340 embracer conifer PFT₂: purple line; deciduous trees PFT₃: gray thick line) observed in the model for the
1341 North American boreal communities (parameter values as in Tab. 2).

1342

1343 **Figure 3.** Community state maps (see color legend) observed for individual parameter variations, for the
1344 Mediterranean (left), tropical (center) and boreal (right) communities. Black vertical lines represent the
1345 reference values in Tab. 2. Parameters were individually changed from 0.5 (Low) to 2 (High) times their
1346 reference value, except for fire responses (R_i) that were changed between 0.01 (Low) and 0.9 (High).

1347

1348 **Figure 4.** Community state maps (see color legend) observed in the parameter plane of the fire response
1349 of PFT₁, R_1 (x-axis) in combination with either the colonization rate of PFT₂, c_2 (A, C, E) or the
1350 colonization rate of PFT₁, c_1 (B, D, F) for (A-B) Mediterranean, (C-D) humid tropical and (E-F) Boreal
1351 communities. The parameter reference values (Tab. 2) are identified by the black crosses.

1352

Figure 1

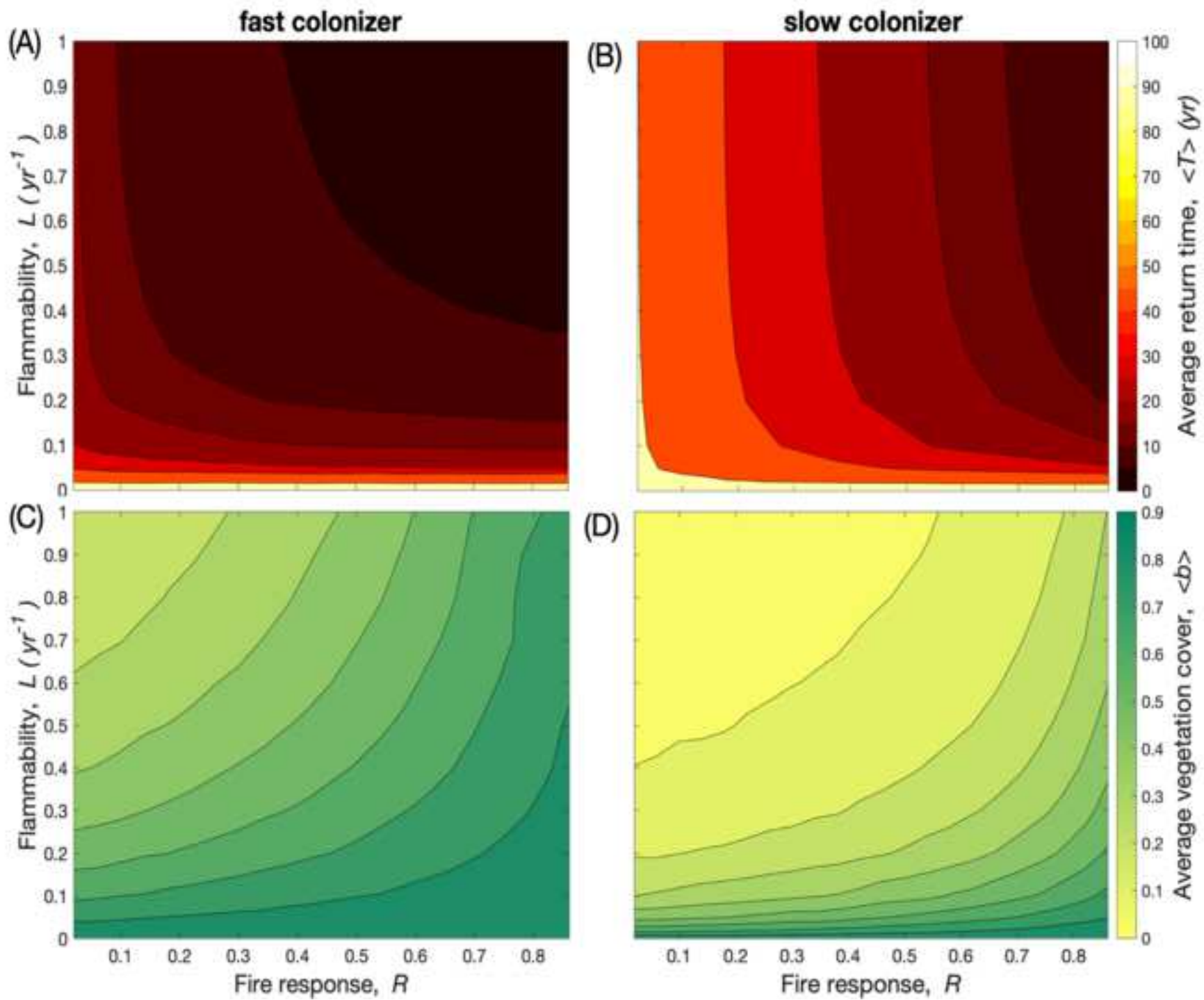


Figure2

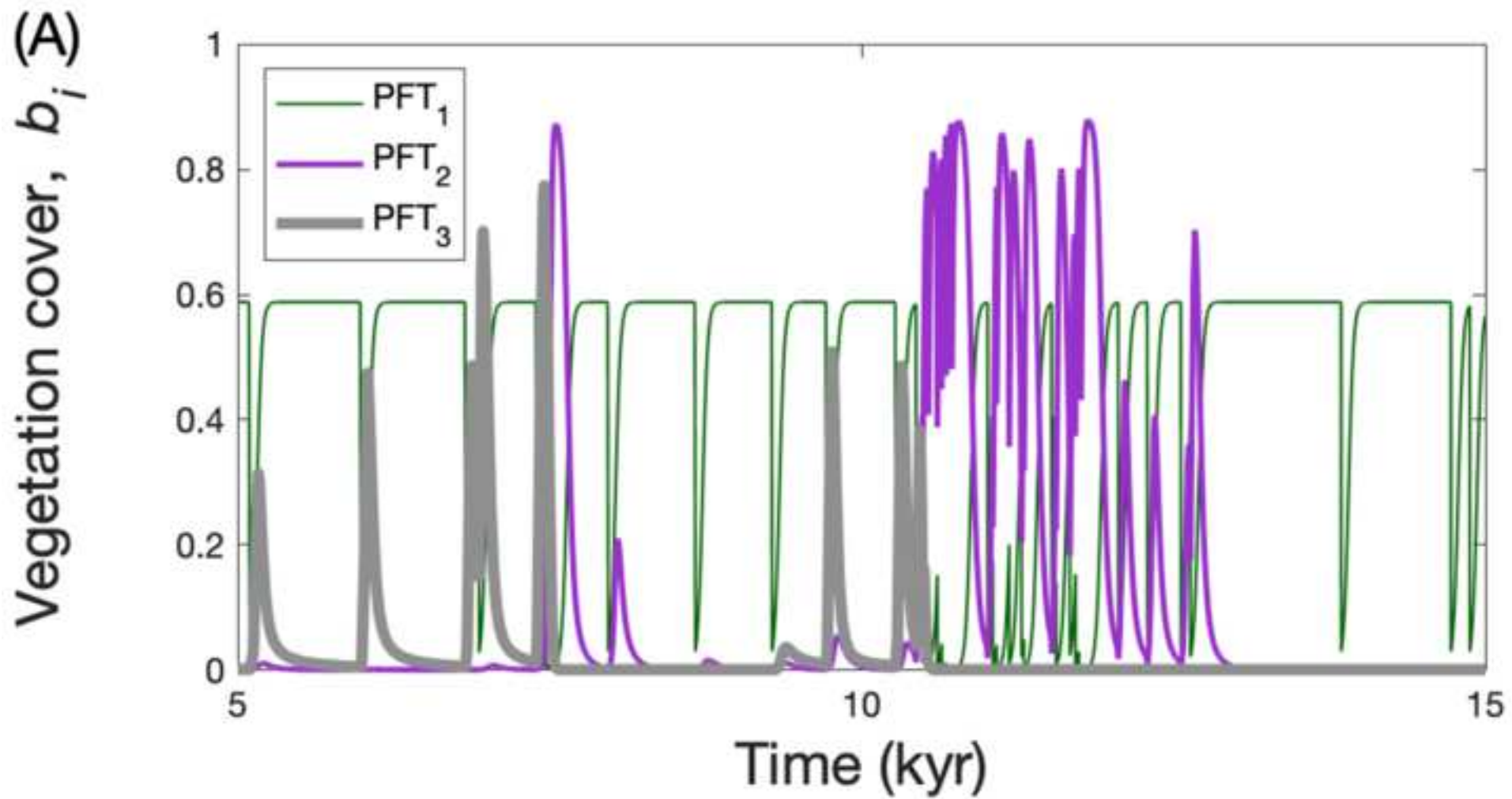


Figure 3

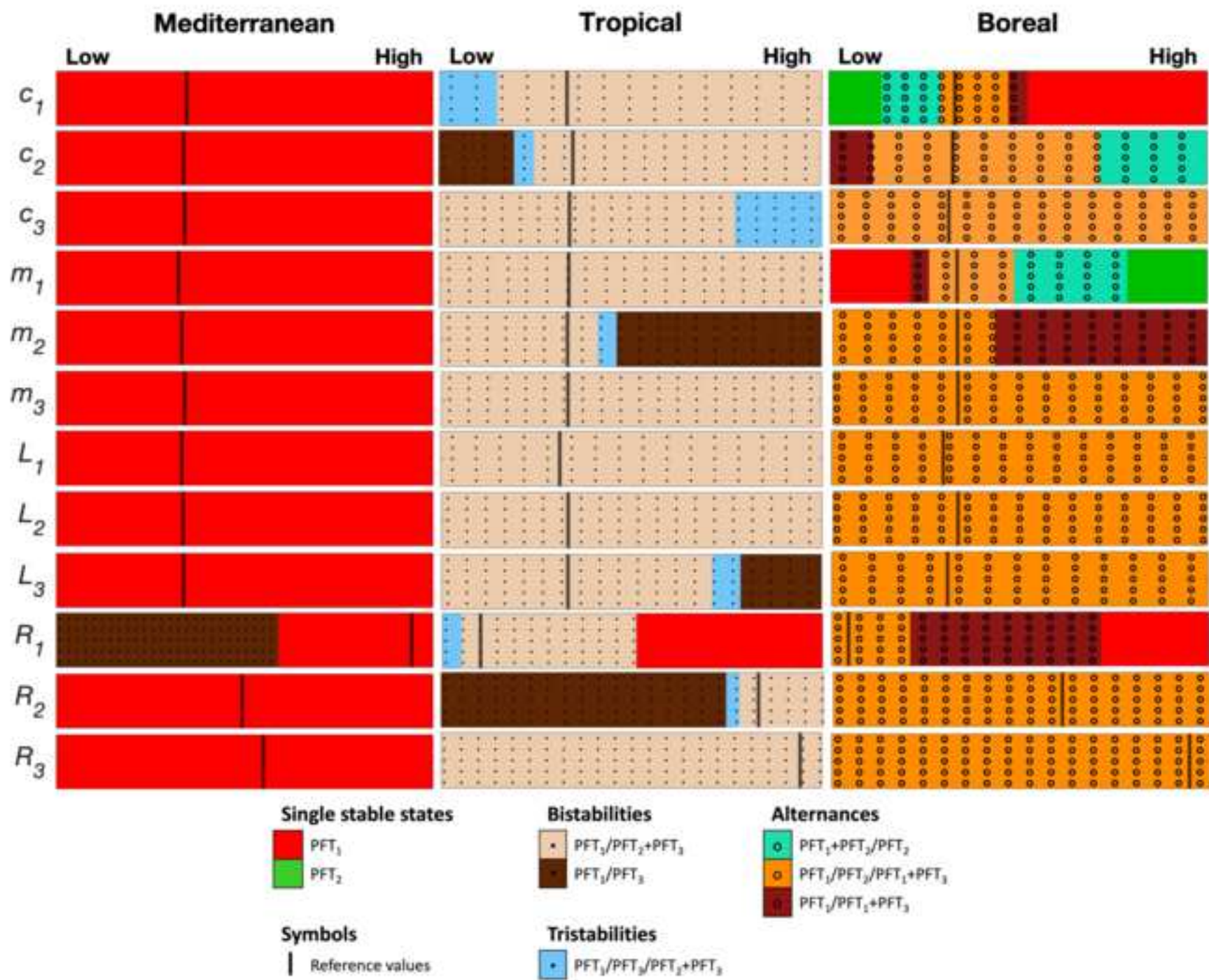
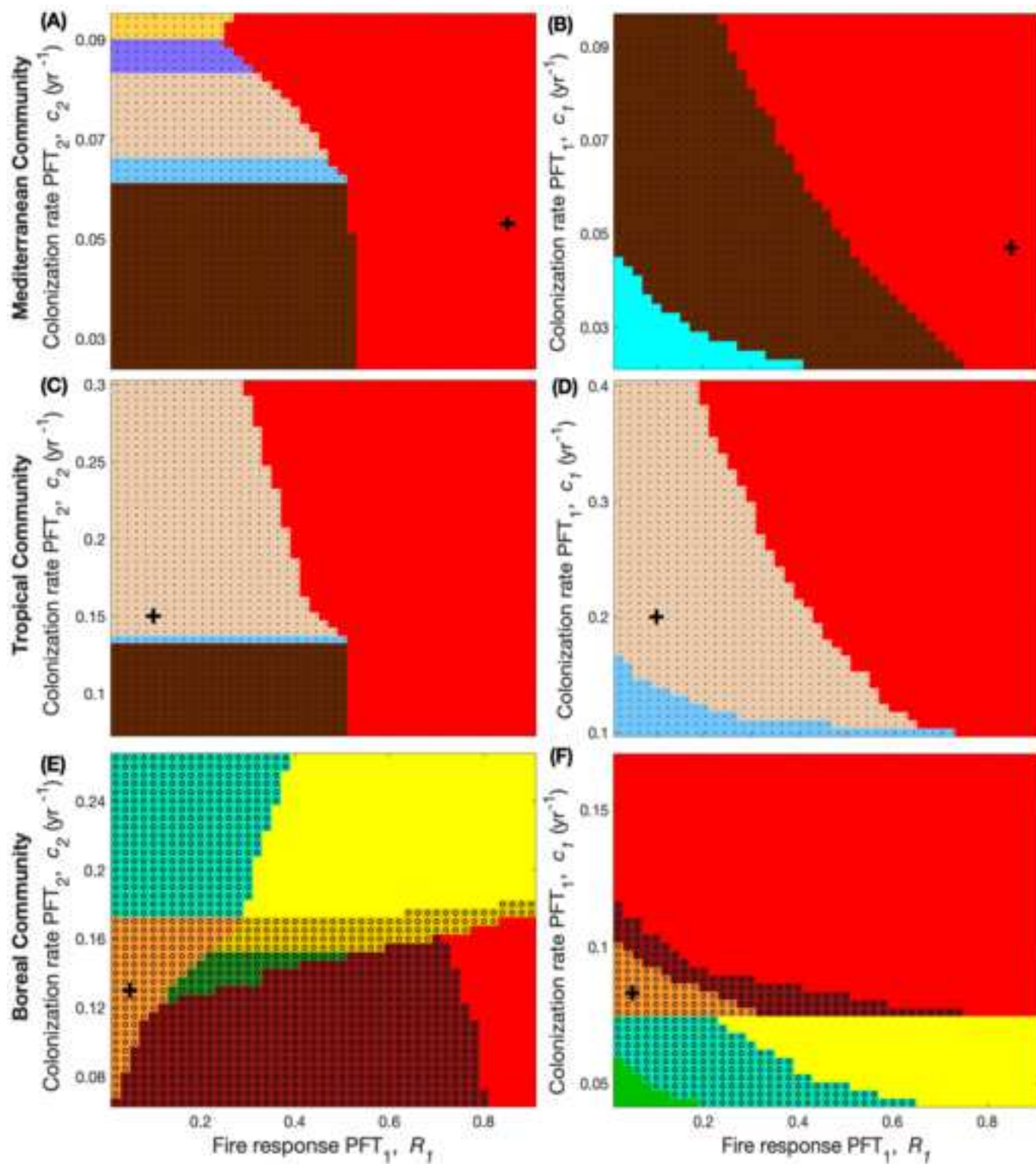
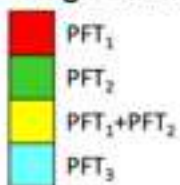


Figure4



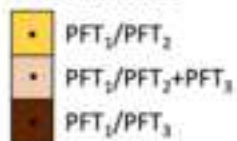
Single stable states



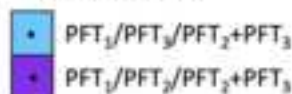
Symbols

⊕ Reference values

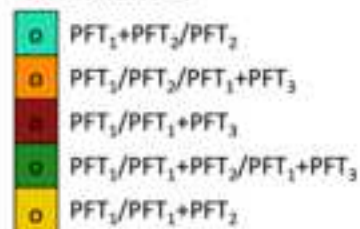
Bistabilities



Tristabilities



Alternances



Appendix

A. Derivation of non-dimensional equations

We derived the non-dimensional version of Eq. (1)-(3) in order to define a plant intraspecific competition parameter. Using the following rescaling

$$u_i = \frac{c_i b_i}{c_i - m_i} ; i = 1,2,3 \quad (\text{A1})$$

$$\tau = t (c_1 - m_1)$$

with u_i the rescaled vegetation cover of PFT_{*i*} and τ the non-dimensional time, Eq. (1)-(3) became

$$\frac{du_1}{d\tau} = u_1(1 - u_1) , \quad (\text{A2})$$

$$\frac{du_2}{d\tau} = \rho_2 u_2(1 - a_{21}u_1 - u_2), \quad (\text{A3})$$

$$\frac{du_3}{d\tau} = \rho_3 u_3(1 - a_{31}u_1 - a_{32}u_2 - u_3) . \quad (\text{A4})$$

Here we defined:

$$\rho_i = \frac{c_i - m_i}{c_1 - m_1} \text{ with } i > 1, \quad (\text{A5})$$

$$a_{ik} = \left(\frac{c_k - m_k}{c_i - m_i} \right) \frac{c_k + c_i}{c_k} \text{ with } k < i \quad (\text{A6})$$

being ρ_i the ratio of net growth rate of PFT_{*i*} and PFT₁, and a_{ik} the decrease in per-capita colonization rate of PFT_{*i*} caused by PFT_{*k*}, thus quantifying the competition strength of PFT_{*k*} on PFT_{*i*}. Note that, by this non-dimensionalization, the number of free parameters is reduced by one unit compared to Eq. (1)-(3). However, estimating all c_i and m_i of each PFTs remains necessary, in order to define a realistic range of a_{ik} , as these competition parameters are virtually impossible to estimate directly.

Rescaling times and vegetation cover according to (A1), we also defined a non-dimensional average fire return time:

$$\theta_f = \frac{1}{\sum_{i=1}^3 u_i l_i} \quad (\text{A7})$$

Which identifies $l_i = L_i/c_i$ as the non-dimensional flammability of PFT_{*i*}.

Universal rescaling in PFT experiments

In ‘PFT experiments’ we studied the dynamics of the PFTs one at a time, by setting the cover of other PFTs to zero. Eq. (A4) defines a universal rescaling of plants flammability. Hence, Figure 1 would be invariant for any PFT. We repeated the experiments of Section 3.1, by running the dimensional model for different PFTs changing the flammability (L) and growth rate (c) of the dimensional model (Eq. 1-3) so to maintain the rescaled flammability ($l=L/c$) constant. Then, we rescaled the vegetation cover according to Eq A1. In order to show the invariance of Figure 1, we represented in Figure A1 the average rescaled vegetation cover ($\langle u \rangle$) versus fire response (R), which would correspond to curves along horizontal lines identified at different values of L in the representation of Figure 1. The rescaled vegetation cover of different PFTs having the same non-dimensional flammability (l) collapsed, thus confirming the invariance of Figure 1. The proof was repeated for two different values of mortality rate (Figure A1a and A1b) keeping the growth rate of the PFTs constant.

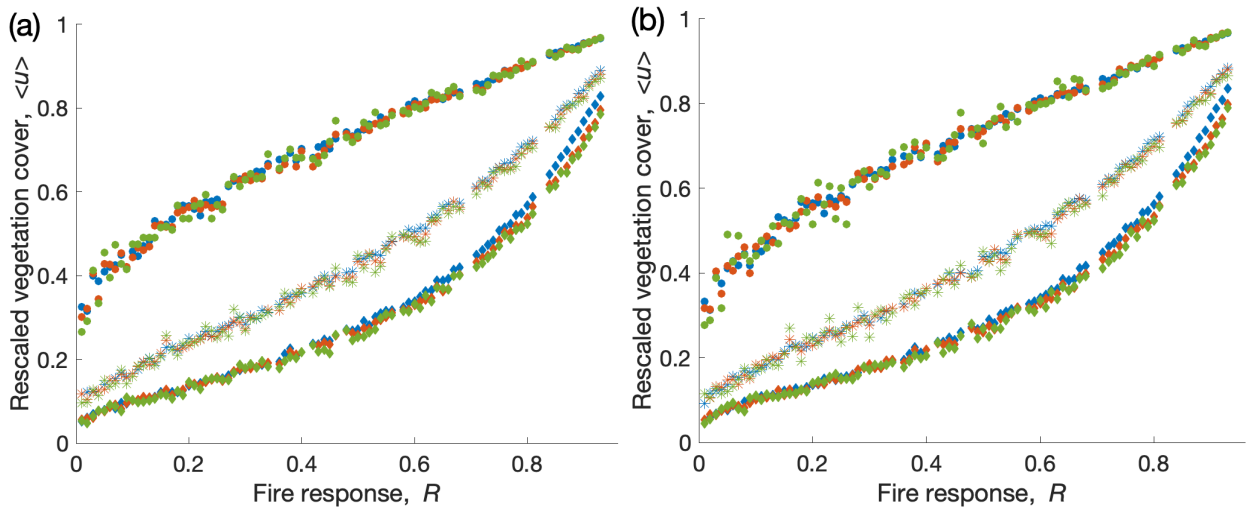


Figure A1. Nondimensional average vegetation cover, $\langle u \rangle$, versus fire response, R , for different PFTs and non-dimensional flammability, $l=L/c$. Dots: $l=1$; stars $l=4$; diamonds $l=8$. (a) Red: $c=0.1 \text{ y}^{-1}$ $m=0.005 \text{ y}^{-1}$; green: $c=0.05 \text{ y}^{-1}$ $m=0.005 \text{ y}^{-1}$; blue: $c=0.025 \text{ y}^{-1}$ $m=0.005 \text{ y}^{-1}$. (b) Red: $c=0.1 \text{ y}^{-1}$ $m=0.01 \text{ y}^{-1}$; green: $c=0.05 \text{ y}^{-1}$ $m=0.01 \text{ y}^{-1}$; blue: $c=0.025 \text{ y}^{-1}$ $m=0.01 \text{ y}^{-1}$.

B. Characteristics of PFTs in the three biomes

Mediterranean biome

Mediterranean forests mostly comprise broad-leaved, sclerophyllous species, with a dominance of Holm oak, *Quercus ilex* (Amici et al., 2013) in the Mediterranean Basin, on which we will focus as a representative example of the Mediterranean biome. These evergreen oaks are late successional, (Clarke et al., 2013; Zeppel et al., 2015) and can outcompete pines and shrubs by the creation of a closed canopy (Acacio et al., 2007; Vayreda et al., 2016). Their understory is typically moist and cool, and they accumulate low amount of fine and dead standing fuel (Puerta-Pinero et al., 2007; Saura-Mas et al., 2009; Tinner et al., 2009; Baeza et al.,

2011; Azevedo et al., 2013). As a result, fires are infrequent in oak forests (fires return time of about 500y, Baudena et al., 2020). In most xeric conditions, oaks are accompanied by conifers as Aleppo pine, *Pinus halepensis*, and Brutia pine, *Pinus brutia* (Zavala et al., 2000; Zavala and Zea, 2004). Fires are more frequent in pine than in oak forests (with average return time of ca. 50y; Baudena et al., 2020), owing to their morphology (Fernandes et al., 2008) and to needle summer senescence, which increases dry fuel accumulation on the ground (Karavani et al., 2018). While Mediterranean oaks are strong resprouters, pines rely upon post fire seed germination (Karavani et al., 2018). The pines' aerial seed bank becomes available early after fires and persists for about 2 y (Pausas, 1999a; Climent et al., 2008). However, pines only produce seeds when mature (after 10 y ca., Pausas, 1999b; Climent et al., 2008). Hence, the survival of the population depends on the presence of adults within dispersal distance (<100 m, Rodrigo et al., 2007) and on fire severity (Fernandes et al., 2008), given that crown fires may affect cones and, even at low intensity fires, their thin juvenile bark will not effectively shield the saplings. In the understory, many shrubs are obligate seeders (e.g. *Rosmarinus officinalis*, *Cistus* spp., *Ulex parviflorus*, etc). Shrubs produce abundant seed banks and their seedlings quickly establish after fire. Succession that has reverted from pine to more flammable shrubs (Hanes, 1971) and stalled in shrublands has been observed (Baeza et al., 2006; Acacio et al., 2009; Santana et al., 2010; Acacio and Holmgren, 2014). Most of the parameters were set following Baudena et al. (2020), in which the model was parameterized and calibrated by means of field measurements from different areas in the Mediterranean basin. In this work, we simplified the model of Baudena and coauthors by including only one understory species, which corresponds to a shrub seeder with characteristics that are averaged among the species considered by Baudena et al.: *Rosmarinus*, *Cistus* or *Ulex* spp.. Similar results are expected for the *Brachypodium retusum*, which is a resprouter grass with intermediate fire response (0.4 in Baudena et al., 2020). Secondly, we avoided implementing an explicit model of seed bank dynamics, as in our model we included only one parameter representing fire response. For seeders, here and in the following case studies, we chose to assign an intermediate range of fire response values ($R_i=0.4-0.55$ ca.). This represents the fact that the recovery of the pine population is fast, though slower than for resprouters, but frequent fires can reduce its seed bank, reducing its overall response (Baudena et al., 2020).

Tropical savannas and forests

Among the fire prone ecosystems, tropical savannas and forests are possibly the most well-known example of two alternative ecological states occurring under the same climatic conditions (e.g. Staver et al 2011, Hirota et al 2011, D'Onofrio et al., 2018; Dantas et al., 2016). Fires were broadly used to justify the maintenance of humid savannas as alternative to tropical forests. In this study, the large shade tolerance of rainforest trees identifies them as the strongest competitor PFT₁, while we choose savanna trees for the PFT₂, and C₄ grass for the PFT₃. Most rain forest species have fire-sensitive trunks (Hoffmann et al., 2012; Dantas et al., 2013) and weak fire response at individual and population level. The wide variety of species that grow within tropical forests is challenging for modelling them (Bampfyle et al., 2005). However, the inter-specific detailed dynamics of rain forest was beyond the aim of this study. Herein, we considered a generic tropical forest tree

as a PFT. These trees are typically long-lived plants (with ages spanning from about 300 y to more than 1000 y, Kurokawa et al., 2003; Laurence et al., 2004). The dense canopy of broad leaves creates a mesic and shady understory and therefore fires are infrequent in tropical forests (average fire occurrence of at least 1000y, see satellite data in D'Onofrio 2018). Under the same climatic conditions, forest trees were showed to grow faster than savanna trees (Viani et al., 2011), owing to a rapid radial growth (Rossatto et al., 2009), a great tolerance of light scarcity provided by the dense canopy (Geiger et al. 2011) and an easy recruitment (San José and Fariñas 1991; Russell-Smith 2004; Geiger et al. 2011). Typical savanna trees are fire-resistant and fire-resilient woody species, with open crown architectures, which preferably grow surrounded by a strongly shade intolerant, flammable grassy understory (Beckage et al. 2009; Warman and Moles 2009; Lehmann et al. 2011; Hoffmann et al. 2012; Dantas et al. 2013). For the parameter values of our model, we used Accatino et al. (2010), which reported values for life span of savanna trees and grasses in the order of 10–100 years and 1–3 years, respectively. The authors estimated the colonization rates of Tilman's model with unlimited water resources, by assuming that it takes 5–100 years for the trees, and 20–180 days for grass to achieve the steady state. We set flammability of trees and grasses to be respectively 5yr and 1-2yr, by using both remote sensing measurement of D'Onofrio et al. (2018) and Accatino et al. (2010), that reposts fire return time spanning from 0.5 to 10yr. Finally, the fire response of grass and trees were chosen considering the added mortality (f and δ_F) in Table 1 of Accatino et al. (2010), being $f=1-R$, with R the fire response of our model. In addition, we accounted for fire related traits of trees, as reported in Table 1.

Boreal biome

In boreal regions, different communities characterize North America and Eurasia, reflecting into different fire regimes (Rogers et al, 2015; Wirth, 2005). Here, we focused on the North America (NA) forests, which mostly include dominant evergreen conifers (e.g., *Abies balsamea*, *Picea spp.*, *Pinus spp.*) and subdominant deciduous trees (e.g., *Betula papyrifera*, *Populus tremuloides*, *Larix Laricina*). The understory of bryophytes and shrubs have mostly a passive role in the fire dynamics (e.g., Klein, 1982; Bergeron et al., 2012), and therefore we did not account for field layer vegetations in this case study. Most information about North American boreal species were obtained from US-FEIS reviews (<https://www.feis-crs.org/feis/>). The colonization rates of boreal PFTs were set by running fire-free simulations for pure stands and using the time of maximal population extension in post fire succession trajectories. In those calibration runs, the initial cover of evergreen seeders was set to $b(t=0)=0.01$ (i.e. nearly total tree burning, in agreement with the stand replacing feature of boreal fires, e.g. Brassard & Chen, 2006), while the deciduous resprouters were assumed to recover within the first growing season after fire, as observed by Zasada et al. (1991) and Greene and Johnson (1999), hence their initial cover was set between $b(t=0)=0.01$ and $b(t=0)=0.40$ (Rogers et al., 2013; Amiro et al., 2001). Among the evergreen conifers, the balsam fir, *Abies balsamea*, is the most shade tolerant, as it was observed to replace spruce- and pine-stands in undisturbed sites (Ali et al., 2008; de Lafontaine et al, 2010, 2012). Hence, balsam fir was chosen as the PFT₁. Balsam fir trees are short-lived (average life span is 90-100y; Uchytel, 1991a; Bergeron, 2000) and fire avoiders (Rogers et al., 2015; Couillard et al., 2018). This species usually prefers

sites characterized by low fire return time (average fire cycle is 250yr in balsam fir stands; Lafontaine et al., 2012). Despite being a prolific seed producer, balsam fir is among the least fire-resistant conifers in North America (Sirois, 1997): seeds are not retained on trees and are often destroyed by fires, owing to the absence of endosperm (Uchyti, 1991a; Rowe and Scotter, 1973). The species recovery relies on rare adult survivors in protected pockets of the forest or neighboring unburned sites (Galipeau et al., 1997). Therefore, this species is usually absent for the first 30-50 post-fire years and eventually reaches maximal abundance 150-200 years after fire (Bouchard et al., 2008; Galipeau et al., 1997). Despite occurring all throughout the NA boreal region, balsam fir is most common in eastern lands (e.g., Uchytil, 1991a). In western regions, white spruce, *Picea Glauca*, is the late successional tree (e.g., Abrahamson, 2015; Rogers et al., 2015). Similar characteristics associate balsam fir and white spruce (Lafontaine et al., 2010; 2012) and therefore the parameterized PFT_1 can also represent the white spruce in the eastern NA boreal regions. Conversions from fir- into spruce-dominated forests were observed in paleoecological records (Couillard et al., 2018; de Lafontaine & Payette, 2010; Ali et al., 2008), matching a shift in the fire frequency. Black spruce, *Picea mariana*, is a moderately shade tolerant tree, which is often accompanied by jack pine, *Pinus banksiana*. Together, black spruce and jack pine account for more than 70% of NA burned area (Rogers et al., 2015). Thus, our PFT_2 represented a spruce-pine mix. In favorable conditions, the life expectancy of black spruce and jack pine is about 200yr (>250yr for black spruce, Bouchard et al., 2008; de Lafontaine & Payette, 2010; and 130-150 for jack pine, Payette et al., 2012). The layered structure and resinous chemical contents render spruce and pine rather flammable trees, with typical fire return-time in spruce and pine forests between 40 yr and 150 yr ca. (Payette et al., 2012; Payette 1992; Larsen 1997; Heon et al., 2014; Wirth, 2005; Amiro et al., 2001; Hart et al., 2019). Black spruce and jack pine are commonly classified as fire embracers (Rogers et al., 2015). Black spruce produces semi-serotinous cones that open soon after fires (Jhonstone et al., 2010; Viereck, 1983) and seeds establishment occur mostly within 3-10 postfire years (Fryer, 2014; Johnstone et al., 2020; Greene & Johnson, 1999). Similarly, the serotinous cones of jack pine open after fires and seed establishment profits of the open canopy, mineral soils and burned duff following fires (Payette et al., 2014; Carey, 1993). Where present in the ground seedbank, black spruce and jack pines become codominant in the community in about 80-90 postfire years (Bouchard et al., 2008), however they are replaced by late successional species, such as balsam fir or northern white cedar without fires. Deciduous trees are generally the most shade intolerant species in NA communities (Bouchard et al., 2008), therefore they were represented by the PFT_3 . For the parametrization, we referred to the most common species: paper birch, *Betula papyrifera*, and trembling aspen, *Populus tremuloides*. Paper birch and trembling aspen are pioneer species (Bergeron, 2000), with average life span of 130yr (less than 140yr for birch and about 120yr for aspen; Uchytil, 1991b; Howard, 1996). These species are rare in late successional communities, and usually restricted to openings (Mack et al., 2021). Pure stands in burned-over lands reach the maximum extension in 30-40 yr after a wildfire and persist for about 40-100 yr (Rogers et al., 2013; Brassard & Chen, 2006). During these times, a mixedwood community establishes, before being replaced by shade-tolerant conifers (Bergeron, 2000; Bergeron & Fenton, 2012). The high canopy moisture content of live trees makes birch and aspen lowly flammable trees (mean fire return interval between 50 and 150 yr; Larsen,

1997; Swain, 1980; Uchytel, 1991b; Hart et al., 2019). High-to-medium intensity fires usually kill such trees, owing to their extremely thin bark. Nevertheless, paper birch and trembling aspen readily recover after fires through sprouting from the root collar (Greene & Johnson, 1999; Payette, 1993). Sprouting ability declines in Paper birch trees after 40-60 yr, and population recovery relies on prolific seed crops dispersed by wind from undisturbed patch within forests interested by fires (Zasada et al., 1991).

Table B1. Parameterization of colonization rates of the three PFTs considered for each case study of the ‘community emergence’ analysis (Section 3.2).

Biomes	Mediterranean Basin	Humid tropics	Boreal NA
colonization rate of PFT ₁ , c_1	published estimates of <i>Quercus spp.</i> from Baudena et al. (2020): c_1 from Table 2 therein	information about growth and spread rates of forest trees, also compared to savanna PFTs (San José and Fariñas 1991; Russell-Smith 2004; Rossatto et al., 2009; Geiger et al. 2011; Viani et al., 2011)	regrowth and steady state achievement time after severe fires in <i>Abies balsamea</i> (Bouchard et al., 2008; Galipeau et al., 1997)
colonization rate of PFT ₂ , c_2	published estimates of <i>Pinus halepensis</i> from Baudena et al. (2020): c_2 from Table 2 therein	parameterized value of savanna trees from Accatino et al. (2010): γ_T from Table 1 therein	regrowth and steady state achievement time after severe fires in <i>Picea mariana</i> and <i>Pinus Banksiana stands</i> (Fryer, 2014; Bouchard et al., 2008)
colonization rate of PFT ₃ , c_3	average value of <i>Rosmarinus officinalis</i> , <i>Ulex parviflorus</i> and <i>Cistus spp.</i> from Table 2 of Baudena et al. (2020): c_3 - c_5 therein	parameterized value of savanna grasses from Accatino et al. (2010): γ_G from Table 1 therein	regrowth and steady state achievement time after severe fires in <i>Betula papyrifera</i> and <i>Populus tremuloides</i> stands (Rogers et al., 2013; Brassard & Chen, 2006; Bergeron, 2000; Bergeron & Fenton, 2012)

References

Klein, D. R. (1982). Fire, lichens, and caribou Rangifer tarandus, ecological diversity, Eurasia, North America. *Rangeland Ecology & Management/Journal of Range Management Archives*, 35(3), 390-395.

C. Fire distribution

In this appendix we present the characteristics of the fire distribution, the numerical implementation of the stochastic process and the resulting fire series. Finally, we discuss the effect of extreme fire events (i.e. randomly long or short interarrival times) in fostering state transitions in the simulations.

Fire events were represented as a nonstationary Poisson process. A Poisson process is a renewal point process in which the number of events occurring within a certain time interval follow a Poisson distribution. Such process is generally characterized by interarrival times that are exponentially distributed. The exponential distribution is identified by one parameter only: the average interarrival time. When the Poisson process is nonstationary, the average interarrival time is state dependent and therefore the shape of the exponential distribution changes in time (as in d'Odorico et al., 2006).

In the fire case, the interarrival times are often called fire return intervals (FRIs). Let us define:

- T_f , which is an instantaneous and deterministic value provided by Eq. (4); this is the *a priori* average return time from which the fire events are generated, and it changes across the simulation, depending on the community composition (Fig. C1);
- FRIs, which are the stochastic realized values observed in the simulations;
- $\langle T \rangle$, which is the observed average value of the FRIs in a given time interval of the simulation; the $\langle T \rangle$ computed over a certain time interval of the simulation tends to its deterministic value $T_f(b_i(t), L_i)$

To represent the Poisson process in the simulations, we used the fact that such a process can either produce or not a fire event at each time step dt , and thus it can be viewed as the result of an independent Bernoulli process with occurrence probability $P=dt/T_f$. In other words, once the value of the deterministic average interarrival time (T_f) is computed, a fire event can randomly occur or not in each time step and the probability of occurrence is higher when T_f is lower.

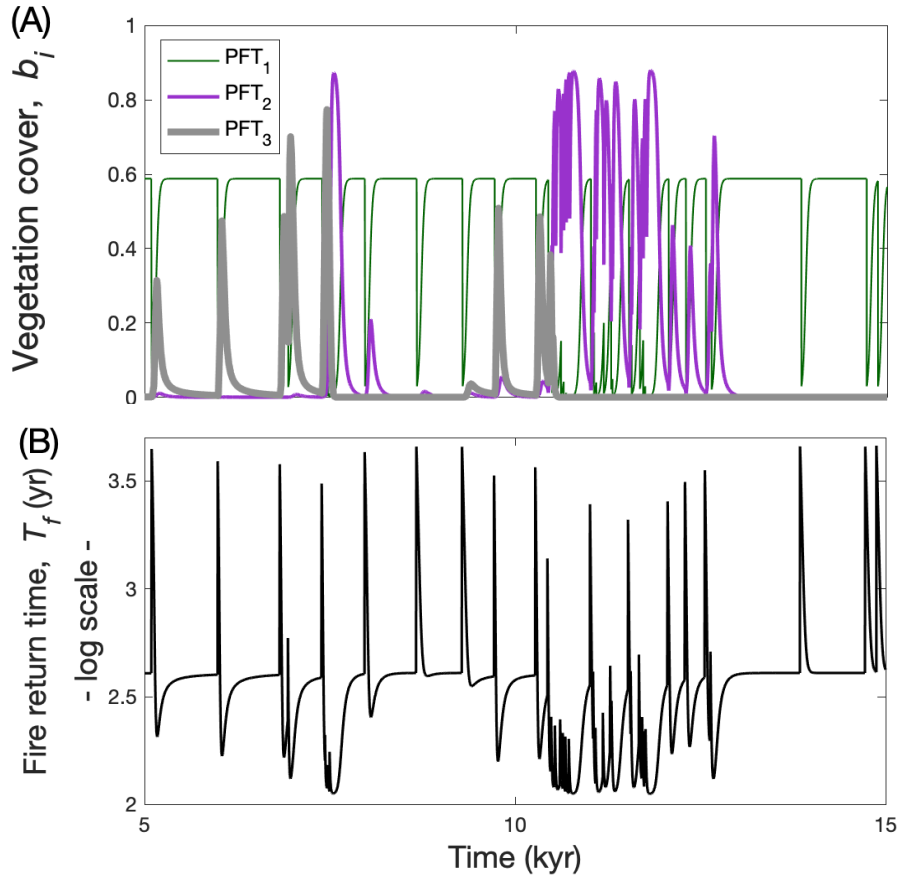


Figure C1. Example of time series of (A) vegetation cover (same as Fig. 2) and (B) the instantaneous fire return time T_f , computed from Eq. (4) for the parameterized boreal community (Tab. 2).

Realized distributions of fire return intervals and number of events

A typical (i.e., average) fire return time characterized each state in the parameterized communities (Tab. 2). In Fig. C2-3, we reported two examples respectively for the Mediterranean and tropical communities (corresponding to the black crosses in Fig. 4A-B and Fig4C-D), where we excluded the initial 3kyr to leave out the transients of the simulations.

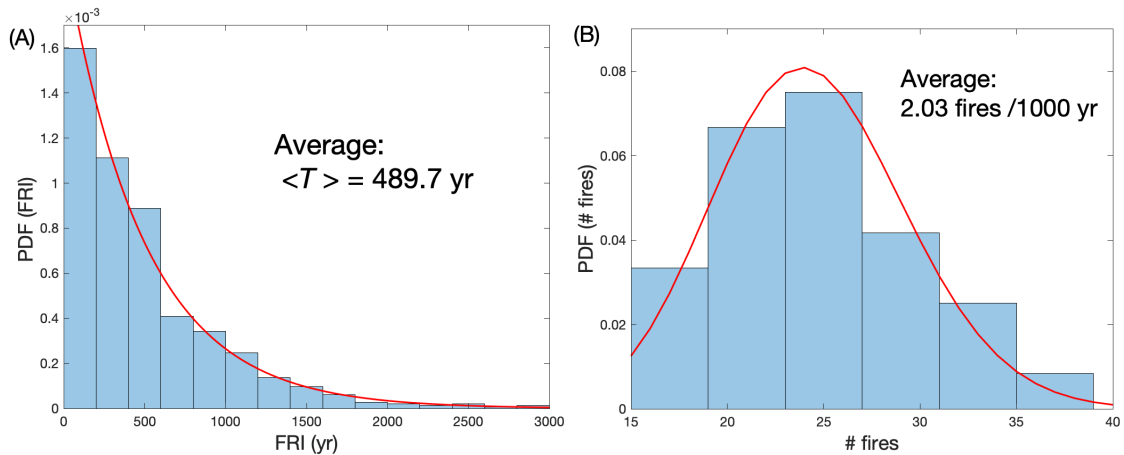


Figure C2. Distribution of (A) FRI and (B) number of events obtained for the black cross in Fig. 4A-B, Mediterranean case study. Distributions are normalized as Probability Density Functions (PDF). Average values reported on the panels are the mean values as provided by either the distribution fit or the computation of the algebraic mean value.

In the tropical case study, where the parameterized community is bistable, we report separately the exponential and Poisson distributions for the tropical forest (PFT_1 , Fig. C3A-B) and savanna (PFT_2+PFT_3 , Fig. C3B-D). Similarly, we obtained an exponential and Poisson distribution for each of the states involved in the irregular alternations for the boreal case study (black crosses in Fig. 4E-F). In the boreal case, the average fire return intervals $\langle T \rangle$ were 445yr, 80 yr and 97 yr for PFT_1 , PFT_2 and PFT_1+PFT_3 states respectively.

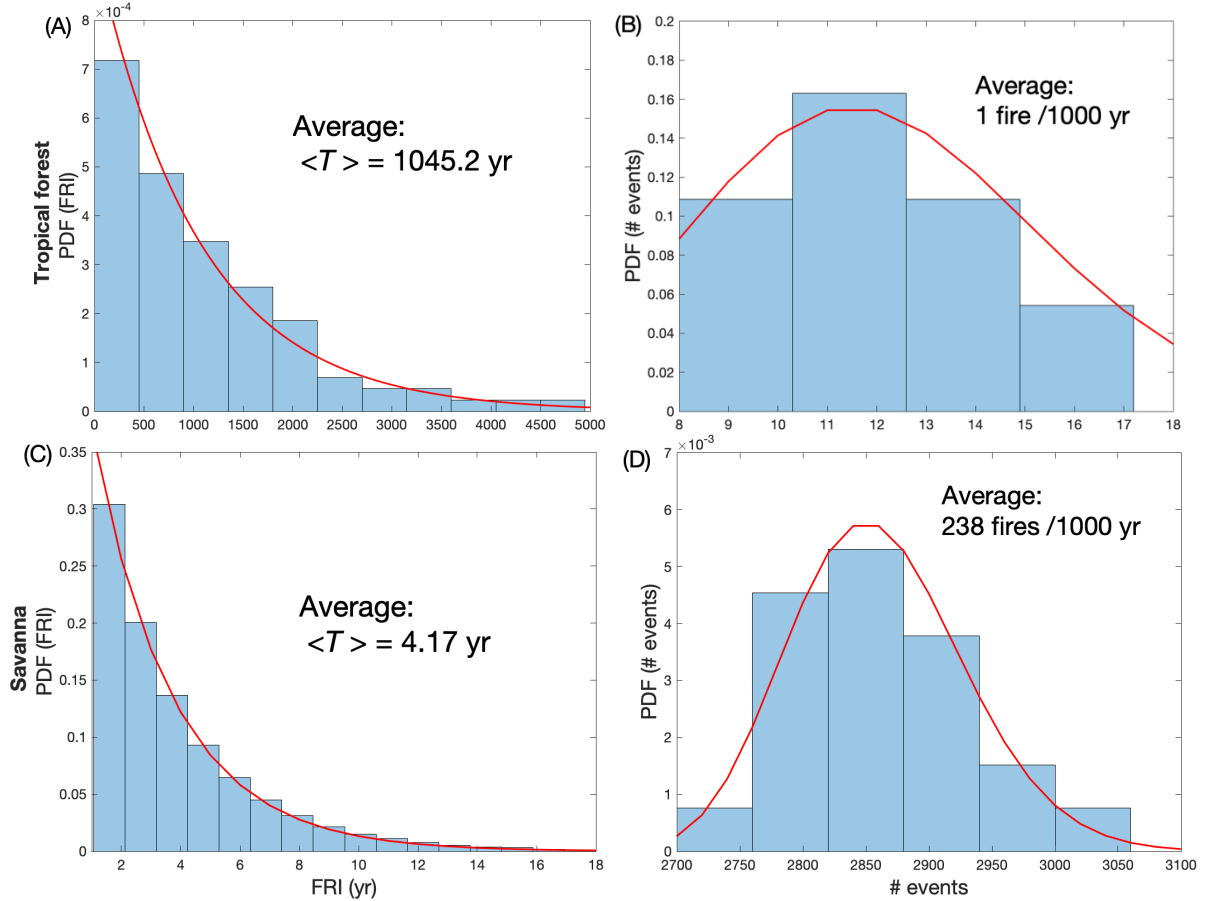


Figure C3. Distribution of (A-C) FRI and (B-D) number of events obtained for the black cross in Fig. 4C-D, tropical case study. Same conventions as in Fig. C2. Notice the different scales on the x-axis for the savanna and forest cases. In the tropical forest example (panel A) the longest FRI was 22 yr, while in the savanna example (panel C) the maximum FRI was 38 yr, but we restricted the x-axis range up to 18 yr for visualization reasons.

Extreme fire return intervals trigger transitions

To illustrate the importance of very short or long fire return intervals, we ran a set of simulations in which we imposed fire events with either short or long return time, to see whether such sequences would trigger transitions.

Very long or very short FRIs (compared to the average FRI) fostered the transition between states across the simulation time. For instance, transitions from tropical forest (PFT_1) to savanna (PFT_2+PFT_3) occurred for sporadically short FRIs, as long as $b_2 \neq 0$ and $b_3 \neq 0$. Similarly, very long FRI favored the transition from PFT_2+PFT_3 to PFT_1 state, if $b_1 \neq 0$ at the time when those events occurred. This can be observed in Fig. C4A-C where we show a simulation where a tropical forest has established, and savanna grasses and trees have low

cover ($b_2 = b_3 = 0.0001$). At a certain point in time, we imposed three fire events separated by short FRIs (namely 20 yrs; identified by the black arrows in Fig. C4C). Afterwards, we left the system to freely evolve. As it is clearly visible in Fig. C4A, the three imposed fires caused a transition from forest to savanna. Vice versa, considering a simulation with an established savanna and a very low cover of tropical forest ($b_1 = 0.001$; Fig. C4B-D), and imposing three fire events separated by very long FRIs (100 yr; black arrows in Fig. C4D), we observed a transition from a savanna to a tropical forest. In both cases, one or two short/long FRIs ensured the state transition, as in the case of real simulations.

We highlight here that such a process played a relevant role only in the initial part of the simulations or required an external input of fire events. Otherwise, in the long runs, when a community (e.g. the tropical forest) became dominant, the cover of the other plants (e.g. savanna PFTs) asymptotically dropped to 0, $b_i \rightarrow 0$, and therefore the established community was maintained in time. In the case of irregular alternances, the transition between states occurred across the whole simulation time and state changes were again associated with randomly short or long FRI, as can be intuitively seen in Fig. C1 (e.g., between 10 kyr and 13 kyr). In such a case, none of the PFT cover tended asymptotically to 0, thus they always had a possibility to regrow at a later time.

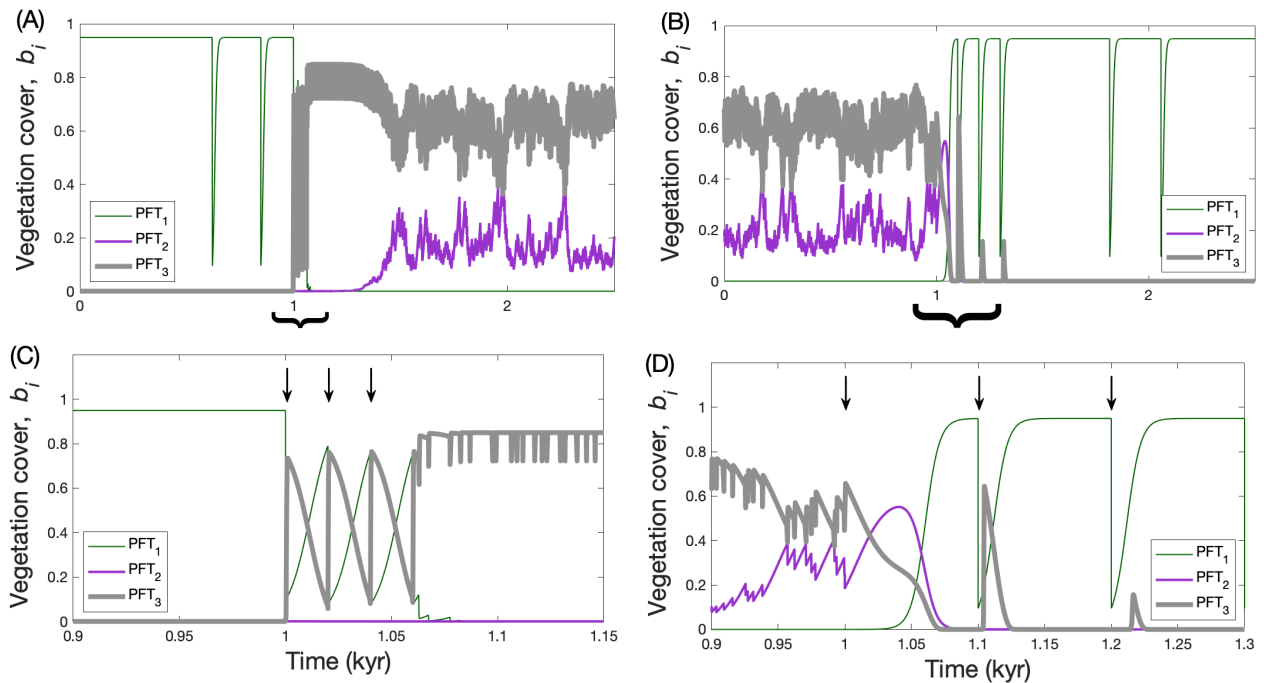
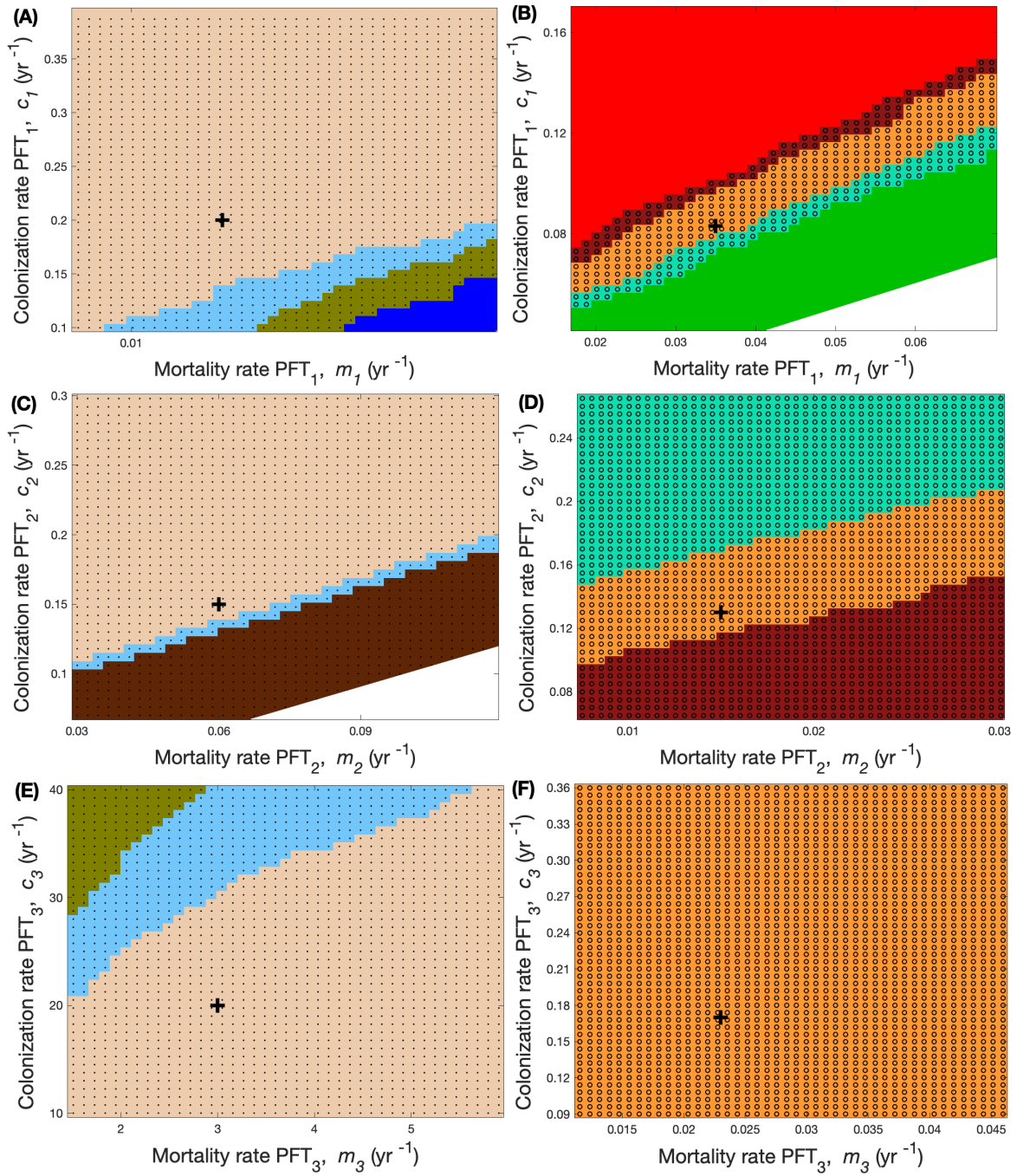


Figure C4. Examples of time series of (A-C) a transition from forest to savanna, and (B-D) a transition from savanna to forest. Panels (C) and (D) are respectively zooms of panels (A) and (B) around the time when fires were imposed with artificial return times (identified by the back brackets). Fire events imposed to foster the transition are marked by black vertical arrows.

D. Community sensitivity analyses

Colonization-mortality rate relationship in tropical and boreal communities



Single stable states

- PFT₁
- PFT₂
- PFT₂+PFT₃

Symbols

- + Reference values

Bistabilities

- PFT₁/PFT₂+PFT₃
- PFT₁/PFT₃
- PFT₃/PFT₂+PFT₃

Tristabilities

- PFT₁/PFT₃/PFT₂+PFT₃

Alternances

- PFT₁+PFT₂/PFT₂
- PFT₁/PFT₂/PFT₁+PFT₃
- PFT₁/PFT₁+PFT₃

Figure D1. Relationship between colonization (c_i) and mortality (m_i) rates for PFT₁ (top: A,B), PFT₂ (center: C,D) and PFT₃ (bottom: E,F) obtained from parameter sensitivity analysis in tropical (left: A,C,E) and boreal (right: B,D,F) communities. Black crosses correspond to the parameterized values (Table 2). White areas correspond to regions where $c_i < m_i$. See Sec. 2.3.2 for further details.

Relationship between the colonization rate of PFT₁ (c_1) and the colonization rate of PFT₂ (c_2)

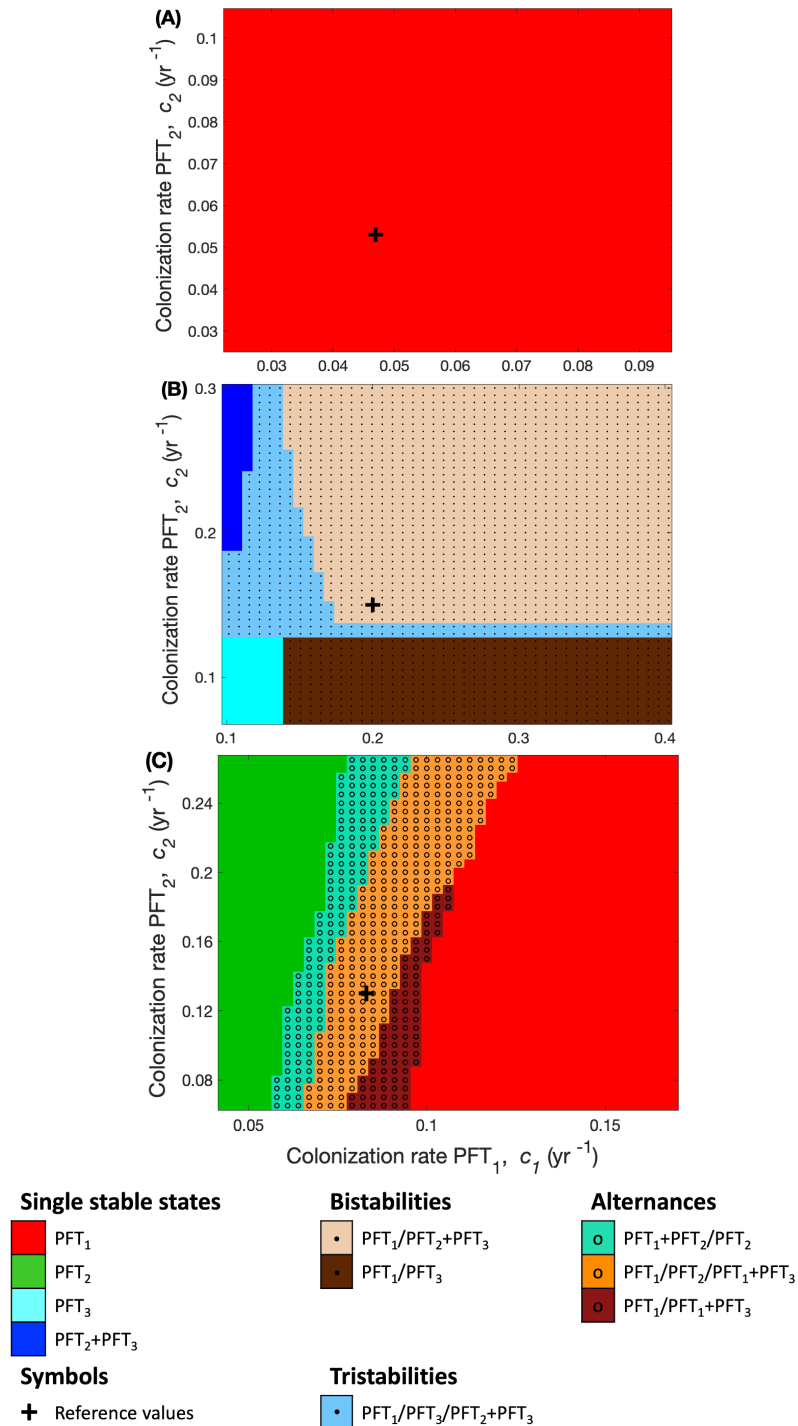
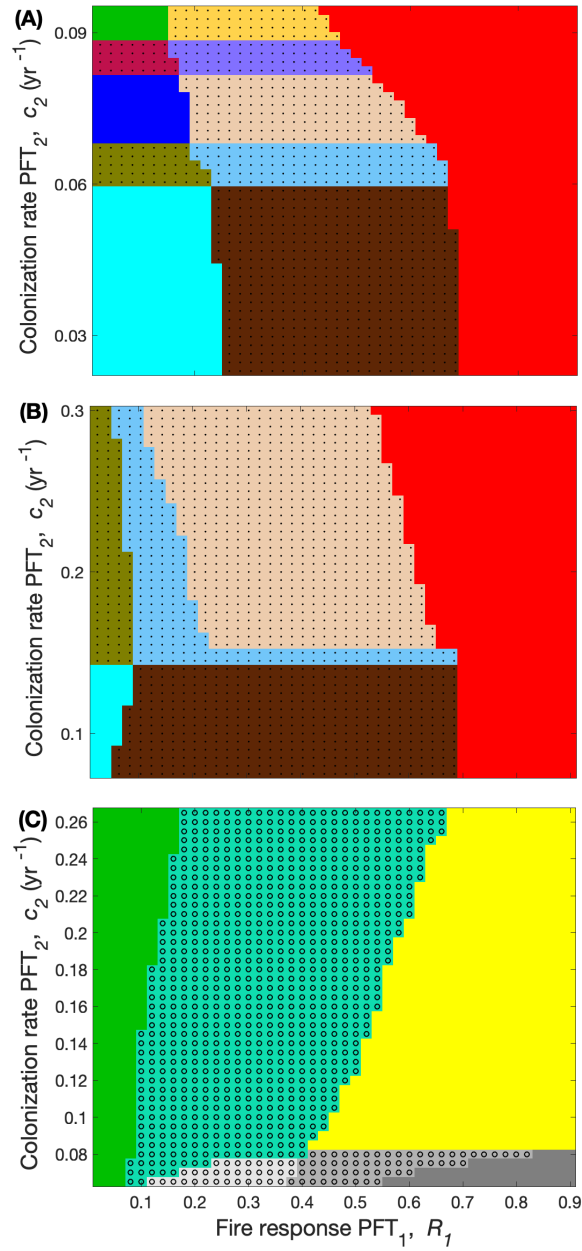


Figure D2. Ecological states maps (see colour legend) in the neighborhood of the parameterized values (Table 2) for (A) Mediterranean, (B) humid tropical and (C) boreal communities as observed in the parameter plane of the growth rate of PFT₁, c_1 (x-axis) and the growth rate of PFT₂, c_2 (y-axis).

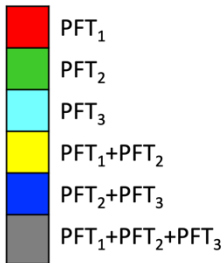
Relationship between fire response of PFT₁ (R_f) and the colonization rate of PFT₂ (c_2) at reduced colonization rate of PFT₁ (c_1)

Expanding the parameter space around the colonization rate of PFT₂ and the fire response of PFT₁, while reducing the colonization rate of the strongest competitor PFT₁ at the same time, we observed that the patterns of states of Figure 4A,C,E seemingly shifted towards larger R_f . Here, results are shown at c_1 reduced to 0.6 time its reference value (Tab. 2).

In all panels, new stable states in which PFT₁ eventually disappeared emerged at low fire response values of the PFT₁, R_f . Hence, fire intolerant PFT₁ was lost if its colonization ability was reduced, despite its advantaged condition in the community. On the other hand, the stable PFT₁ forest was preserved at large R_f in the Mediterranean and tropical communities, and also in the boreal communities, though accompanied by PFT₂. Recalling the reference values of R_f in the Mediterranean community (Table 2), we remark that a closed canopy forest of holm oak would be preserved also if its colonization rate was reduced, because of its strong fire response. However, a concomitant reduction of R_f to intermediate values would lead the oak forest to become bistable with other states, including pines and shrubs together or separately, which is a similar result to that found by Baudena et al. (2020). Conversely, the fire intolerant tropical forest would be lost in consequence of a reduction of its colonization rate and would be replaced by a savanna or grassland (possibly bistable between them). Similarly, the fire avoider balsam fir would disappear as a consequence of a reduction of its colonization rate. For the boreal case, we also notice that the stable PFT₁ forest disappears from the parameter plane and in any case the PFT₁ forest alone is never present as a state in the irregular alternation (Fig. C3C).



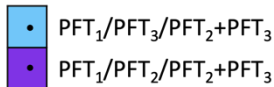
Single stable states



Bistabilities



Tristabilities



Alternances

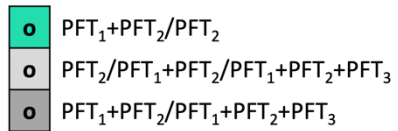


Figure D3. Ecological states maps (see colour legend) in the neighborhood of the parameterized values (Table 2) for (A) Mediterranean, (B) humid tropical and (C) boreal communities as observed in the parameter plane of fire response of PFT₁, R_1 (x-axis) and the growth rate of PFT₂, c_2 (y-axis) for the growth rate of PFT₁, c_1 reduced to 0.6 times its reference values.