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1 **A trade-off between embolism resistance and bark thickness in**  
2 **conifers: are drought and fire adaptations antagonistic?**

3

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15

## 16 **Abstract**

17 **Background:** Understanding the mechanisms that explain the spatial distribution  
18 of conifers across biogeographical gradients is important for anticipating  
19 potential range shifts owing to global change. Classical explanations have  
20 involved trade-offs between shade and drought tolerances, but more recent  
21 studies observed that trade-offs between fire and drought tolerances could also be  
22 important.

23 **Aims:** Here we propose that a contributing mechanism to explain how conifer  
24 species are distributed across productivity gradients – with marked variation in  
25 the incidence of fire - involves a trade-off between allocation to bark, which  
26 serves to protect against fire, or to embolism resistance, which serves to protect  
27 against drought.

28 **Methods:** We compiled information from different datasets and performed  
29 regression analyses.

30 **Results:** We observed a trade-off between bark thickness and embolism  
31 resistance in conifer species such that species show either large investments of  
32 carbon to the bark or have thinner barks but xylem resistant to embolism; we did  
33 not observe conifer species concomitantly showing high fire tolerance and  
34 embolism resistance.

35 **Conclusions:** This study serves as a starting point for a novel framework on how  
36 fire and drought adaptations affect conifer biogeography. Additional studies will  
37 be necessary to discover the generality of our findings by including other species  
38 of conifers, e.g. those in the Southern Hemisphere.

39 **Keywords:** bark, cavitation, climate change, conifers, fire, drought, life strategies,  
40 trade-off

## 41 **Introduction**

42 Variation in fire regimes (pyrogeography) across biomes is primarily driven by  
43 productivity and aridity gradients (Boer et al. 2016). Maximum global fire activity  
44 occurs at intermediate levels of productivity and aridity. Conversely, minimum fire  
45 activity is observed at sites with low productivity and high aridity (i.e. deserts, with  
46 strong fuel limitation), or at sites with high productivity and low aridity (i.e. wet

47 temperate/tropical forests, where the large amounts of accumulated biomass are seldom  
48 dry enough to burn) (Keeley et al. 2012; Pausas and Bradstock 2007; Pausas and  
49 Ribeiro 2013).

50         Considering these interactions between productivity and aridity as drivers of  
51 pyrogeography, Keeley (2012) has proposed a division of life strategies across the  
52 species of *Pinus*, later expanded by Pausas (2015), and classified species in relation to  
53 fire as tolerant, embracer and avoider. Fire-tolerant species occur at the more productive  
54 sites, where fire activity is often limited by high moisture that results in low intensity  
55 surface fires (Figure 1). Consequently, fire-tolerant species (e.g. *P. nigra*, *P. ponderosa*,  
56 *P. sylvestris*) have thick barks that allow the survival of individuals under low intensity  
57 fires, but do not regenerate under high intensity crown defoliating fires. Fire-embracer  
58 species occur at sites with intermediate productivity, where fire activity is highest, and  
59 have a low degree of self-pruning and an overall canopy architecture that enhances  
60 crown fires (Figure 1). Their regeneration depends on stand-replacing fires that open  
61 their serotinous cones (e.g.: *P. attenuata*, *P. halepensis*). Fire-avoider species occur at  
62 dry (or upper montane) environments, where fires are very rare and limited by fuel load  
63 (or moisture), and lack adaptations to fire (e.g.: *P. aristata*, *P. uncinata*; Figure 1).

64         The analyses of trade-offs among traits have been useful to explain species  
65 distributions across productivity gradients (Rueda et al. 2016; Valladares et al. 2016).  
66 Here we elaborate on a mechanism that could explain, at least partly, recently reported  
67 trade-offs in the ability to cope with stress (drought) and disturbance (fire) in conifer  
68 species (Karavani et al. 2018; Rueda et al. 2016). We hypothesised that adaptations to  
69 fire and drought incurred a cost and that conifers might not concomitantly survived  
70 disturbance and stress. Thus, conifer species may either show large investments of  
71 carbon to the bark, which protects the cambium and phloem against fire; or have thinner

72 barks and xylem highly resistant to embolism. Consequently, we hypothesised that  
73 conifer species concomitantly showing high bark thickness and embolism resistance  
74 may not occur. There are many traits involved in fire tolerance and drought resistance,  
75 but bark thickness and embolism resistance are of pivotal importance.

76 We begin by providing some basic calculations on the carbon costs of  
77 constructing bark and xylem resistant to embolism. We then revisit recent work  
78 indicating the potential for a trade-off between fire resistance and drought tolerance  
79 (Karavani, et al. 2018). Further, we test for the existence of a trade-off in embolism  
80 resistance and bark thickness. Finally, we explain the relevance of our findings in a  
81 broader context of conifer biogeography.

## 82 **The carbon cost of constructing bark and xylem**

83 The presence of a trade-off in the allocation of C to either building fire-resistant bark or  
84 drought-resistant xylem is conditional on the existence of substantial construction costs.  
85 Fernandes et al. (2008) have reported normalised bark thickness (the ratio of bark  
86 thickness to stem radius) in western European pines ranging from 7.4% in *P. uncinata*  
87 to 24.5% in *P. pinaster*; bark density is ca. 90% that of the xylem in pines (Miles and  
88 Smith 2009). Assuming that C concentration is similar across tissues (ca. 50% in both  
89 cases (Chave et al. 2009; Hansson et al. 2004)), it thus follows that resources consumed  
90 by the bark range from ca. 6.7 % ( $7.4 \times 0.9$ ) to 22.1 % ( $24.5 \times 0.9$ ) those of the xylem,  
91 thus representing a substantial construction cost.

92 In terms of embolism resistance, different adjustments of tracheid anatomy and  
93 morphology occur for different conifer families. In species of the Pinaceae and  
94 Cupressaceae (which largely dominate our analyses), wood density and tracheid  
95 ‘thickness-to-span’ ratio are strongly correlated with protection from drought-induced  
96 embolism (Pittermann et al. 2006). Consequently, mechanical strength is required in

97 these species to avoid tracheid collapse under drought and the correlation between  
98 density and resistance to embolism indicates that these trees incur substantial C costs  
99 during xylem construction [i.e.: higher wood density leads to higher embolism  
100 resistance; (Pittermann, et al. 2006)]. In fact, recent studies have demonstrated that the  
101 amount of lignin, which varies between 25 and 36% of wood dry mass in conifers  
102 (Fengel and Grosser 1975; Pettersen 1984), is directly related to embolism resistance.  
103 Pereira et al. (2017) have observed a significant correlation between the values of  $\Psi_{50}$   
104 (the xylem potential where 50% of the hydraulic conductivity is lost) for different  
105 species (Choat et al. 2012) with their respective lignin concentrations (Fengel and  
106 Grosser 1975; Pettersen 1984). Based on such correlation, they quantified that an  
107 increase of 1% of dry mass allocation to lignin reduced  $\Psi_{50}$  by -0.3MPa.

#### 108 **Evidence for trade-offs in embolism resistance and fire tolerance in conifers**

109 The existence of a trade-off between fire tolerance and cavitation resistance in conifer  
110 species may be tested with previously published datasets. Data on embolism resistance  
111 were obtained from a global database (Choat, et al. 2012). We used  $\Psi_{50}$  as this is a  
112 commonly used indicator of embolism resistance in conifers (Brodribb and Cochard  
113 2009). We collected data on fire tolerance from the USDA PLANTS database  
114 ([www.plants.usda.gov](http://www.plants.usda.gov), 13 Dec 2016). This database provides a value on “the relative  
115 ability to resprout, regrow, or re-establish from residual seed after a fire”, and there are  
116 four possible levels (none, low, medium, high). After crossing the two datasets, we were  
117 able to examine hydraulic resistance and fire tolerance across 41 conifer species (Table  
118 S1). No species from those present in the database was able to resprout.

119 In this analysis we found evidence for a trade-off between  $\Psi_{50}$  and fire tolerance  
120 (Figure 2a). Conifers with xylem more resistant to embolism (e.g. with  $\Psi_{50} \leq -6$  MPa,

121 and down to -12MPa) had either low or no tolerance to fire (levels 1-2 in Figure 1a),  
122 whereas conifers with mid or high fire tolerance (levels 3-4 in Figure 2a) always  
123 showed smaller embolism resistance (e.g. with  $\Psi_{50} > -5$  MPa) (Figure 2a). We also  
124 observed some conifer species with low resistance to cavitation and low tolerance to fire  
125 but there were no species showing both high fire tolerance and high  $\Psi_{50}$  (Figure 2a).  
126 Despite the scatter in the data, the lack of conifers concomitantly showing high fire  
127 tolerance and high embolism resistance points towards a trade-off between these two  
128 traits.

129         As proposed by Grubb (2016), the existence of trade-offs may be formally  
130 demonstrated through quantile regression (when fitting an upper quantile the regression  
131 becomes significant). Consequently, we examined the significance of the 0.5, 0.75 and  
132 0.95 quantiles and found only the 0.95 quantile regression significant ( $P < 0.05$ ) (using  
133 the “quantreg” package (Koenker 2016) within the R software environment (R Core  
134 Team 2016)), hence suggesting a trade-off between  $\Psi_{50}$  and fire tolerance in conifers  
135 (Figure 2a). We note that using different datasets could introduce additional uncertainty  
136 around mean trait values. However, this problem affected equally all species and should  
137 not lead to any systematic bias.

### 138 **Evidence for trade-offs in embolism resistance and bark thickness in conifers**

139 The previous analysis is not exempt of criticism because of the ambiguous definition of  
140 fire tolerance in the USDA PLANTS database. To overcome this limitation, we  
141 conducted further analyses with independent sources of information to test the specific  
142 hypothesis that there was a trade-off in the allocation of resources to the bark or to  
143 embolism resistance. First, we digitised data on resistances to cambium kill from a  
144 previous study on fire resistance across European pines (Fernandes, et al. 2008). This

145 allowed the examination of six species in total (Table S1), a small number, but  
146 representing a substantial proportion of the pines in Europe (Barbéro et al. 1998; Willis  
147 et al. 1998). Cambium kill resistance in the study by Fernandes, et al. (2008) was  
148 derived from the percentage of tree radius occupied by bark (at 1.3 m). We observed a  
149 negative relationship between resistance to cambium kill and  $\Psi_{50}$  (Figure 2b), which is  
150 consistent with our hypothesis of a trade-off.

151 We additionally used an independent dataset on bark thickness at a normalised  
152 stem diameter of 10 cm across 20 conifer species (Table S1) from a recent global study  
153 (Pellegrini et al. 2017). We observed again that species with a thicker bark were least  
154 resistant to embolism and there were no species concomitantly showing thick bark and  
155 high embolism resistance (Figure 2c). While more data would be needed to generalise  
156 this claim, the trade-off is formally anticipated by the significant (at  $P < 0.05$ ) 0.95  
157 quantile regression.

158 We also addressed patterns of intra-specific genetic variation underlying a  
159 potential trade-off between drought and fire tolerances by digitising graphs with data on  
160 bark thickness (Tapias et al. 2004) and on  $\Psi_{50}$  (Corcuera et al. 2011) for six different  
161 provenances of *P. pinaster* grown under uniform conditions. This Mediterranean pine  
162 has a very broad ecological niche (from sea level to 1900 m), which has elicited  
163 adaptive divergence among populations arising through localised selection (González-  
164 Martínez et al. 2004). The provenances spanned a broad precipitation (348 - 1,257 mm  
165  $\text{yr}^{-1}$ ) and soil fertility gradient (mainly acid soils, but also basic soils and even sandy and  
166 poor soils such as those of Landes, France). From a fire perspective this species is  
167 important as a large proportion of all fires in the western Mediterranean basin occur in  
168 *P. pinaster* stands. In Spain alone, one-third of all forest fires have been reported from  
169 forests dominated by this species (MAGRAMA 2012). This dataset, at intra-specific



170 level, once more indicated a negative relationship between bark thickness and  $\Psi_{50}$  was  
171 also significant (Figure 2d).

## 172 **Conclusions and outlook**

173 Overall, our analyses using independent datasets and across different geographical  
174 scales indicate that there are no conifers concomitantly showing high embolism  
175 resistance and high tolerance to fire and that this may be owing to an C allocation trade-  
176 off between bark and lignin. Moreover, the intra-specific association observed for *Pinus*  
177 *pinaster* under common-garden conditions (Figure 2d) indicates that this trade-off has a  
178 genetic basis, although further studies on genetic variation would be required to  
179 generalise this claim.

180 Our hypothesis on a trade-off between embolism resistance and fire tolerance  
181 raises the question as to whether adaptations to fire and to drought may, at least to some  
182 degree, be antagonistic in conifers. This hypothesis is still tentative because many  
183 additional mechanisms, including stomatal regulation, root:shoot allocation or stem  
184 capacitance to name a few, are also involved in drought resistance. However, it could  
185 provide a mechanistic explanation, at least partially, to the distribution of the species of  
186 *Pinus* and, in general, conifers with different life strategies across productivity gradients  
187 (Rueda, et al. 2016).

188 Further studies should address the role of site fertility as an additional driver of  
189 productivity. From the perspective of pyrogeography, productivity gradients have so far  
190 been defined as precipitation gradients (Pausas and Bradstock 2007). However, site  
191 productivity is also a function of nutrient concentrations and that could be particularly  
192 important for species that occur across a wide range of soil nutrient availabilities (e.g.:  
193 *P. pinaster*, *P. sylvestris*, *Larix laricina*, *Taxodium distichum*, etc). This is particularly

194 important because nutrient concentrations tend to decrease xylem vulnerability to  
195 embolism (Ewers et al. 2000; Resco de Dios et al. 2013), although less is known on its  
196 effects on bark production or fire tolerance, and also because of human-induced nutrient  
197 imbalances such as nitrogen deposition (Ochoa-Hueso et al. 2011).

198 Fire-embracing species, that occupy intermediate productivity sites, would need  
199 a high resistance to drought because they are regularly exposed to periods of water  
200 scarcity, but they also live in crown-fire environments and, since non-resprouting trees  
201 often succumb under high intensity crown defoliating fires, any carbon investment into  
202 building structures enhancing fire survival may be futile. Consequently, the mechanism  
203 that allows the maintenance of these species in such environments, rather than cambium  
204 or crown adaptations to withstand fires, relies on a reproductive strategy that ensures  
205 post-fire seed availability via an aerial seed bank (i.e. serotinous cones) (Martín-Sanz et  
206 al. 2016). Similarly, fire-avoiding species from arid environments (e.g. *P. edulis*, *P.*  
207 *monophylla*), which likely show the highest drought tolerance, often lack fire  
208 adaptations (Keeley 2012). Additionally, fire-avoiding upper montane treeline-forming  
209 species which experience cavitation caused by freeze-thaw cycles notably also lack fire  
210 adaptations. Conversely, mesic conifer species need protection from surface fires but  
211 are less exposed to periods of intense drought and, consequently, may preferentially  
212 allocate more resources into protecting the phloem and cambium than the xylem.  
213 Considering forecasts of increased drought and fire occurrence across parts of the  
214 geographical range of temperate conifers (Moritz et al. 2012), understanding conifer  
215 strategies for dealing with these factors should be at the forefront of our research efforts.  
216 Subsequent work should also address the possibility of recovery from cavitation either  
217 by stem refilling or by resprouting.

218

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222

223 **Notes on contributors**

224 Víctor Resco de Dios is interested in understanding biological processes regulating  
225 biosphere-atmosphere interactions.

226 Carles Arteaga is interested in post-fire regeneration processes.

227 Javier Hedo is interested in understanding the effects of fire on forest soils.

228 Eustaquio Gil-Pelegrín is interested in whole-plant ecophysiology of woody plants,  
229 especially in the functional responses of trees and shrubs to drought.

230 Jordi Voltas is interested in understanding adaptive patterns of Mediterranean conifers  
231 and their implications for species resilience under global change

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326

327 Figure legends

328 Figure 1: Idealised and simplified representation of how different conifer functional  
329 groups are distributed across productivity gradients according to a presumed trade-off  
330 between fire tolerance and embolism resistance.

331 Figure 2: Trade-offs between embolism resistance and bark thickness. (a) Relationship  
332 between fire tolerance (1, none; 2, low; 3, medium; 4, high; from PLANTS USGS  
333 database) and the xylem potential where 50% ( $\Psi_{50}$ ) of the hydraulic conductivity is lost  
334 (Choat, et al. 2012) across 41 conifer species. (b) Relationships between cambium and  
335 kill resistance (in relative units) (Fernandes, et al. 2008), against the xylem water  
336 potential where 50% of the hydraulic conductivity is lost ( $\Psi_{50}$ ) (Choat, et al. 2012)  
337 across six European pine species. (c) Relationship between bark thickness for a  
338 diameter of 10 cm (Pellegrini, et al. 2017) against the xylem potential where 50% of the  
339 hydraulic conductivity is lost ( $\Psi_{50}$ ) (Choat, et al. 2012) across conifer species. (d)  
340 Relationship between bark thickness (Tapias, et al. 2004) and  $\Psi_{50}$  (Corcuera, et al.  
341 2011) across six *Pinus pinaster* provenances. The line indicates results of quantile (a, c)  
342 or linear (c, d) regression.  $P$ -values and  $R^2$  are given for quantile and linear regression,  
343 respectively. In quantile regressions, we examined the significance of the 0.5, 0.75 and  
344 0.95 quantile regressions for all plots but only the 0.95 quantile regressions were  
345 significant at  $P < 0.05$ , as indicated by the plotted line. X-axis scales may differ  
346 between panels. (a) modified from (Karavani, et al. 2018).

347