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

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ABSTRACT

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

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

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

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

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

Introduction

Variation in fire regimes (pyrogeography) across biomes is primarily driven by productivity and aridity gradients (Boer et al. 2016). Maximum global fire activity occurs at intermediate levels of productivity and aridity. Conversely, minimum fire activity is observed at sites with low productivity and high aridity (i.e. deserts, with strong fuel limitation), or at sites with high productivity and low aridity (i.e. wet temperate/tropical forests, where the large amounts of accumulated biomass are seldom dry enough to burn) (Pausas and Bradstock 2007; Keeley et al. 2012; Pausas and Ribeiro 2013).

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

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

There are many traits involved in fire tolerance and drought resistance, but bark thickness and embolism resistance are of pivotal importance.

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

The carbon cost of constructing bark and xylem

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

In terms of embolism resistance, different adjustments of tracheid anatomy and morphology occur for different conifer families. In species of the Pinaceae and Cupressaceae (which largely dominate our analyses), wood density and tracheid ‘thickness-to-span’ ratio are strongly correlated with protection from drought-induced embolism (Pittermann et al. 2006). Consequently, mechanical strength is required in these species to avoid tracheid collapse under drought and the correlation between density and resistance to embolism indicates that these trees incur substantial C costs during xylem construction [i.e.: higher wood density leads to higher embolism resistance; (Pittermann et al. 2006)]. In fact, recent studies have demonstrated that the amount of lignin, which varies between 25 and 36% of wood dry mass in conifers (Fengel and Grosser 1975; Pettersen 1984), is directly related to embolism resistance. Pereira et al. (2017) have observed a significant correlation between the values of \( \Psi_{50} \) (the xylem potential where 50% of the hydraulic conductivity is lost) for different species (Choat et al. 2012) with their respective lignin concentrations (Fengel and Grosser 1975; Pettersen 1984). Based on such correlation, they quantified that an increase of 1% of dry mass allocation to lignin reduced \( \Psi_{50} \) by −0.3MPa.

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

The existence of a trade-off between fire tolerance and cavitation resistance in conifer species may be tested with previously published datasets. Data on embolism resistance were obtained from a global database (Choat et al. 2012) with their respective lignin concentrations (Fengel and Grosser 1975; Pettersen 1984). Based on such correlation, they quantified that an increase of 1% of dry mass allocation to lignin reduced \( \Psi_{50} \) by −0.3MPa.
collected data on fire tolerance from the USDA PLANTS database (www.plants.usda.gov, 13 December 2016). This database provides a value on "the relative ability to resprout, regrow, or re-establish from residual seed after a fire", and there are four possible levels (none, low, medium, high). After crossing the two datasets, we were able to examine hydraulic resistance and fire tolerance across 41 conifer species (Table S1). No species from those present in the database was able to resprout.

In this analysis we found evidence for a trade-off between $Ѱ_{50}$ and fire tolerance (Figure 2(a)). Conifers with xylem more resistant to embolism (e.g. with $Ѱ_{50} \leq -6$ MPa, and down to $-12$ MPa) had either low or no tolerance to fire (levels 1–2 in Figure 1(a)), whereas conifers with mid or high fire tolerance (levels 3–4 in Figure 2(a)) always showed smaller embolism resistance (e.g. with $Ѱ_{50} > -5$ MPa) (Figure 2(a)). We also observed some conifer species with low resistance to cavitation and low tolerance to fire but there were no species showing both high fire tolerance and high $Ѱ_{50}$ (Figure 2(a)). Despite the scatter in the data, the lack of conifers concomitantly showing high fire tolerance and high embolism resistance points towards a trade-off between these two traits.

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

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

The previous analysis is not exempt of criticism because of the ambiguous definition of fire tolerance in the USDA PLANTS database. To overcome this limitation, we conducted further analyses with independent sources of information to test the specific hypothesis that there was a trade-off in the allocation of resources to the bark or to embolism resistance. First, we digitised data on resistances to cambium kill from a previous study on fire resistance across European pines (Fernandes et al. 2008). This allowed the examination of six species in total (Table S1), a small number, but representing a substantial proportion of the pines in Europe (Barbéro et al. 1998; Willis et al. 1998). Cambium kill resistance in the study by Fernandes et al. (2008) was derived from the percentage of tree radius occupied by bark (at 1.3 m). We observed a negative relationship between resistance to cambium kill and $\Psi_{50}$ (Figure 2(b)), which is consistent with our hypothesis of a trade-off.

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

We also addressed patterns of intra-specific genetic variation underlying a potential trade-off between drought and fire tolerances by digitising graphs with data on bark thickness (Tapia et al. 2004) and on $\Psi_{50}$ (Corcuera et al. 2011) for six different provenances of *P. pinaster* grown under uniform conditions. This Mediterranean pine has a very broad ecological niche (from sea level to 1900 m), which has elicited adaptive divergence among populations arising through localised selection (González-Martínez et al. 2004). The provenances spanned a broad precipitation (348–1257 mm yr$^{-1}$) and soil fertility gradient (mainly acid soils, but also basic soils and even sandy and poor soils such as those of Landes, France). From a fire perspective this species is important as a large proportion of all fires in the western Mediterranean basin occur in *P. pinaster* stands. In Spain alone, one-third of all forest fires have been reported from forests dominated by this species (MAGRAMA 2012). This dataset, at intra-specific level, once more indicated a negative relationship between bark thickness and $\Psi_{50}$ was also significant (Figure 2(d)).

**Conclusions and outlook**

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

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

Further studies should address the role of site fertility as an additional driver of productivity. From the perspective of pyrogeography, productivity gradients have so far been defined as precipitation gradients (Pausas and Bradstock 2007). However, site productivity is also a function of nutrient concentrations and that could be particularly important for species that occur across a wide range of soil nutrient availabilities (e.g. *P. pinaster, P. sylvestris, Larix laricina, Taxodium distichum*, etc). This is particularly important because low nutrient concentrations tend to decrease xylem vulnerability to embolism (Ewers et al. 2000; Resco De Dios et al. 2013), although less is known on its effects on bark production or fire tolerance, and also because of human-induced nutrient imbalances such as nitrogen deposition (Ochoa-Hueso et al. 2011).
Fire-embracing species, that occupy intermediate productivity sites, would need a high resistance to drought because they are regularly exposed to periods of water scarcity, but they also live in crown-fire environments and, since non-resprouting trees often succumb under high intensity crown defoliating fires, any carbon investment into building structures enhancing fire survival may be futile. Consequently, the mechanism that allows the maintenance of these species in such environments, rather than cambium or crown adaptations to withstand fires, relies on a reproductive strategy that ensures post-fire seed availability via an aerial seed bank (i.e. serotinous cones) (Martín-Sanz et al. 2016). Similarly, fire-avoiding species from arid environments (e.g. P. edulis, P. monophylla), which likely show the highest drought tolerance, often lack fire adaptations (Keeley 2012). Additionally, fire-avoiding upper montane treeline-forming species which experience cavitation caused by freeze-thaw cycles notably also lack fire adaptations. Conversely, mesic conifer species need protection from surface fires but are less exposed to periods of intense drought and, consequently, may preferentially allocate more resources into protecting the phloem and cambium than the xylem. Considering forecasts of increased drought and fire occurrence across parts of the geographical range of temperate conifers (Moritz et al. 2012), understanding conifer strategies for dealing with these factors should be at the forefront of our research efforts. Subsequent work should also address the possibility of recovery from cavitation either by stem refilling or by resprouting.

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Víctor Resco de Dios is interested in understanding ecological processes regulating biosphere-atmosphere interactions.

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

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

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