Title:

Canopy self-replacement in *Pinus sylvestris* rear-edge populations after drought-induced die-off.

Running title: *P. sylvestris* self-replacement after die-off event

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Summary

In recent years, *Pinus sylvestris* die-off and mortality events have occurred across all its range of distribution, usually associated with recurrent droughts induced by climate change. A shift in terms of canopy dominance by other better adapted co-existing species can be expected, especially in populations located close to their climatic tolerance limits. Herein, we test along a local elevational gradient whether canopy opening resulting from die-off favours the growth of a non-dominant co-existing tree species (*Q. pubescens*) established in the understorey, in comparison to *P. sylvestris*. We also test whether the growth of both species is associated with local climatic suitability for these species or, alternatively, with direct measures of micro-climatic variables. Finally, the effect on tree growth of other micro-local factors such as competition, canopy closure or micro-topography was tested. Understorey tree growth was overall enhanced by canopy opening resulting from *P. sylvestris* die-off and defoliation, but this response was stronger in *P. sylvestris* trees, supporting self-replacement of this species after the die-off. This higher growth rate is related to modifications in micro-local climate (higher temperatures in the wettest quarter), Conversely, *Q. pubescens* is less sensitive to micro-local climate conditions but it can grow faster than *P. sylvestris* on stands with no canopy defoliation. In contrast, climatic suitability extracted from SDMs was negatively related to understorey *P. sylvestris* growth and had no effect on *Q. pubescens*. These contrasting results support observations at plot scale that *P. sylvestris* self-replacement is better explained by local environmental conditions than by values of climatic suitability obtained from regional-scale data-sets. Nevertheless, these climatic suitability measures remain consistent with the overall pattern of replacement at seedling level observed at the rear edge of the species' distribution. This study reveals that, at local scale, short-term shifts of species dominance will not necessarily occur in the studied *P. sylvestris* forests. This finding reinforces the notion that micro-local environment and species traits (i.e., light and temperature tolerance, life-history strategies) modulate the resilience capacity in rear-edge populations that otherwise could be expected to be prone to collapse.

1. Introduction

Anthropogenic global change is responsible for global warming, as well as being the main cause of the increase in both the frequency and severity of extreme climatic events such as droughts and heatwaves (IPCC, 2013; Trenberth et al., 2014). Forest die-off and mortality (Allen et al., 2015; Anderegg et al., 2015) have been recorded across all the forested biomes in parallel with recurrent regional droughts accompanied by high temperatures, probably induced by the aforementioned global changes. The causes of such mortality are mainly related to physiological mechanisms related to water deficit, such as hydraulic failure and carbon starvation (Adams, Zeppel, Anderegg, Hartmann, Landhäusser, Tissue, Huxman, McDowell, et al., 2017; McDowell et al., 2018), although other agents such as pests can also intervene (f.e. Lloret and Kitzberger 2018). From a demographic perspective, forest resilience after episodes of drought-induced mortality is largely determined by the ability of non-dominant trees or saplings previously established in the understorey to replace canopy trees affected by die-off (Batllori et al., 2020; Martínez-Vilalta & Lloret, 2016). In turn, this replacement could be determined by the suitability of climate conditions for the growth of potential replacing species and by stand structural characteristics, reflecting resource availability and species interactions (Lloret, Jaime, Margalef-Marrase, Pérez-Navarro, & Batllori, 2021).

Species distribution models (SDMs) are statistical models that provide the probability of appearance, by relating species occurrence to environmental spatial data, often of a bioclimatic nature (Guisan & Thuiller, 2005). They can therefore be used to characterize species' bioclimatic niches and thus the suitability of the climatic conditions that populations experience across their distribution ranges. Moreover, climatic suitability derived from SDMs is habitually used to predict vegetation dynamics under changing climatic conditions (Dobrowski et al., 2011; Koo et al., 2017). At a regional scale, a relationship between climatic suitability derived from SDMs and drought-induced die-off has been established (Lloret & Kitzberger, 2018;

Margalef-Marrase et al., 2020). Moreover, climatic suitability has proved useful at community level for comparing the responses in different co-occurring species to extreme events driven by climate change (Pérez Navarro et al., 2018; Sapes et al., 2017). These models could therefore serve as a tool for standardizing population responses in the face of extreme climatic conditions, which in turn determine their capacity for resilience. Significantly, micro-local environment (Thuiller et al., 2014) and yearly climatic variability (Perez-Navarro et al., 2020) – not captured in most climate databases – could modulate demographic responses at local scale. While suitability indices can better explain populations responses at regional scale than climatic variables, at local scale climatic and bioclimatic variables such as mean annual precipitation, monthly temperature or monthly precipitation have been associated with tree growth and survival (Bogino, Fernández Nieto, & Bravo, 2009; Hereş et al., 2012).

In the last two decades, *Pinus sylvestris* L. (Scots Pine) forests have experienced die-off and mortality events across the distribution range of this species. This phenomenon has been attributed to the increasing of both temperature and drought recurrence and intensity resulting from climate change (Sánchez-Salguero et al., 2012; Thabeet et al., 2009; Vacchiano, Garbarino, Borgogno Mondino, & Motta, 2012). Tree mortality has particularly impacted *P. sylvestris* populations living on the southernmost edge of its distribution in the Iberian Peninsula (Galiano et al., 2010; Matías & Jump, 2012; Sánchez-Salguero et al., 2012), which are expected to suffer climatic conditions closer to the species' tolerance limit (Sánchez-Salguero et al., 2017). Furthermore, other local non-climatic factors such as stand structure (Vilà-Cabrera et al., 2011), pests (Jaime et al., 2019), mistletoe infestation and soil quality can exacerbate the progression of die-off (Galiano, Martínez-Vilalta, & Lloret, 2010). In these rear-edge populations of *P. sylvestris*, resilience determined by self-replacement following mortality can be affected by a further reduction in micro-local climatic suitability due to the structural characteristics of stands after canopy loss. In contrast, the establishment of species other than the previously dominant *P. sylvestris*, such as *Quercus* spp., may be enhanced (Galiano et al., 2013), probably because they find better climatic suitability under these stand-level structural changes. However, the successful emergence and establishment of seedlings cannot be directly translated into forest canopy shifts due to species replacement. The survival rates of *P. sylvestris* seedlings are usually extremely low, and they are substantially affected by micro-local habitat conditions, particularly fluctuating herbivore pressure (Castro et al., 2004). In conclusion, the early stages of population establishment, though a necessary step for long-term dynamics, provide little information about short-term forest dynamics after die-off episodes, which should be more closely linked to the fate of saplings and sub-canopy trees (Batllori et al., 2021; Lloret et al., 2021).

In this study, we aim to elucidate tree-level growth, which probably determines self-replacement or, alternatively, replacement by other existing tree species, in forests dominated by *P. sylvestris* which have experienced drought-induced tree die-off and mortality. These populations are situated in the Pre-Pyrenees (Northern Iberian Peninsula), which spread through the southern limit of the *P. sylvestris* distribution range. Here, we use both climatic suitability extracted from SDMs and micro-local bioclimatic variables directly measured in the field to study the growth performance of trees belonging to different species and located in the forest understorey. These growth patterns would help to predict the forest's short-term dynamics at stand level. Specifically, we compare the individual growth of both *P. sylvestris* and *Quercus pubescens* WILLD. living below the canopy of *P. sylvestris* trees that reacted to drought in different ways, from total defoliation and dead to maintain green canopy and good health. *Quercus pubescens* is a moderate shade-tolerant species (Niinemets & Valladares, 2006) with a climatic niche distinct from that of *P. sylvestris*, and it can therefore be assumed to present a different suitability on the studied site (Terradas, Estevan, Solé, & Lloret, 2009). We address the following questions:

1. Does the differing degree of the stand-level effect of drought on a canopy – from complete defoliation to good health – influence the growth of trees of the dominant *P. sylvestris* species and the accompanying *Q. pubescens* which are established in the understorey, thus promoting self-replacement or, alternatively, replacement by oaks?

2. Are the die-off induced growth performances of *P. sylvestris* and *Q. pubescens* explained by shifts in micro-local climatic conditions, as estimated either by changes in climatic suitability estimated from SDMs or by *in situ* meteorological records?

3. Does the relationship between the growth patterns of both species and the climatic suitability derived from micro-local conditions change across the altitudinal gradient?

4. Are the different growth patterns of *P. sylvestris* and *Q. pubescens* understorey trees determined by stand-level features such as competition and soil quality, which in turn are determined by drought-induced die-off?

2. Material and methods

2.1. Study Area

This study was conducted in a rear-edge population of *P. sylvestris* located in the Catalan Pre-Pyrenees (Arcalís, Municipality of Soriguera, Spain, WGSA84: 42º 20' 50" N, 1º 5' 20" E). This forest covers a large altitudinal gradient (from 600 to 1,400 m a.s.l., Figure 1) on a North aspect with a medium-to-high slope (10 to 50 % of slope, mean = 30%, see Table S1 of the supplementary material). *Quercus pubescens* appears as a tree species accompanying *P. sylvestris* across all the altitudinal gradient. Other species, such as *Quercus ilex* (holm oak) and *Pinus nigra* (black pine), also occasionally appear in some stands. In these *P. sylvestris* populations, die-off and mortality associated with drought has occurred in recent years, particularly in the years 2005 (Galiano et al., 2010; Jol et al., 2009) and 2012 (Camarero et al., 2018)). This mortality appears in small patches, and spread across the whole altitudinal gradient.

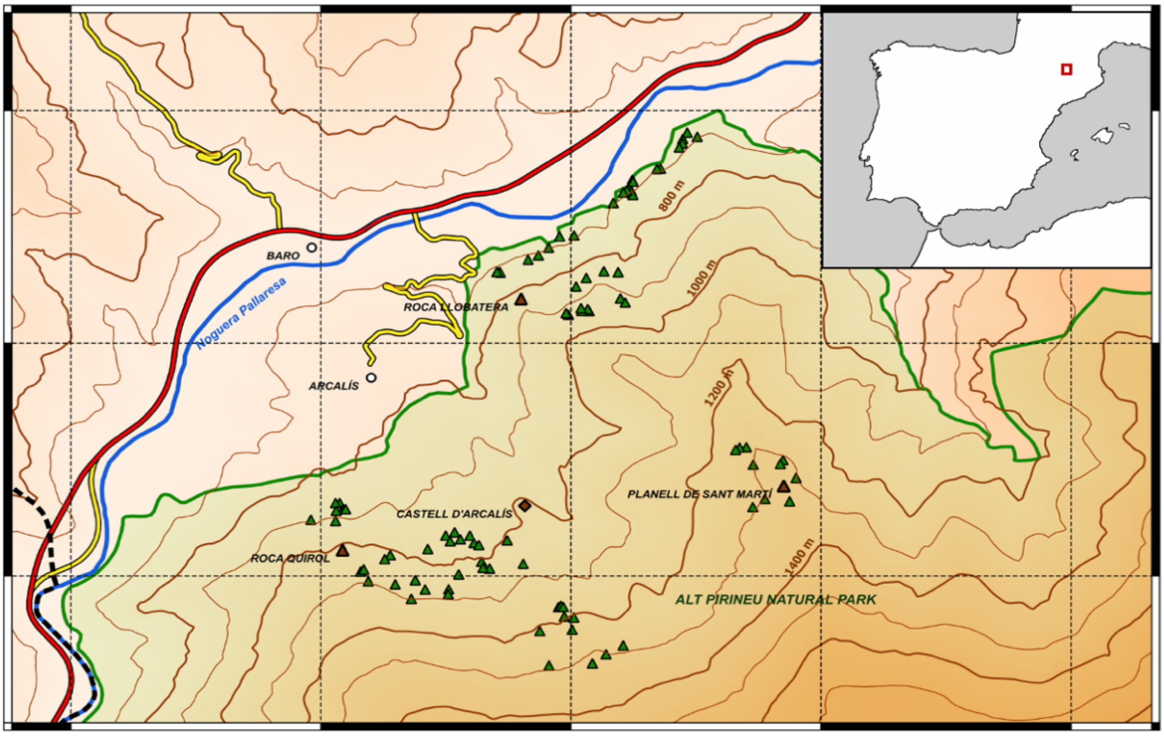

Figure 1: Location of the 88 studied individual trees (green triangles) along the altitudinal gradient in Arcalís Forest (Soriguera municipality, Spain).

2.2. Field data sampling

We selected 44 *P. sylvestris* and 44 *Q. pubescens* understorey trees (7.5 cm. < dbh < 22 cm., See Table S1 of the supplementary material) distributed throughout the elevation gradient. Half of them (22 pines and 22 oaks) were growing under a healthy green canopy of *P. sylvestris* and the other half were growing under a defoliated *P. sylvestris* canopy. The percentage of canopy cover (estimated using a densiometer) was 44% units lower in plots with defoliated canopy than in plots with green canopy (One-way ANOVA, p <0.001, Figure S1). This defoliation (hereafter, defoliated canopy) concurs with the die-off associated with the drought conditions previously reported in this forest (Galiano et al 2010). We characterized the micro-local environment around these sub-canopy trees by establishing 10-metre diameter plots centered on each selected tree. We obtained topographic variables such as slope and orientation. Biotic variables such as basal area (BA), species richness and understorey cover were also extracted after performing a forest inventory in each plot. We also measured and identified all woody individual plants with a 2.5 cm. < dbh inside each plot. Canopy closure was also measured using a densiometer (Fiala, Garman, & Gray, 2006; Strickler, 1959). Finally, micro-local climatic variables (temperature and air relative humidity) were extracted from data loggers located in the north face of the bark of each selected tree 1.5 m above the ground. Tree growth was measured using steel band dendrometers (model DS20, EMS Brno Company), following the manufacturer's protocols, and placing all of them 1.3 m above the ground (breast height). The growth periods considered were the following three years: 2017, 2018 and 2019.

2.3. Competition and water availability

Plant competition could affect tree growth, so at plot level we estimated competition by using stand mean dbh, stand density and basal area (BA). For this purpose, the competition experienced by the selected trees was estimated using the Hegyi competition index (Hegyi, 1974), a distance-dependent index that takes into account the size of the neighbouring trees and their proximity to the selected trees. In our case, we considered all the trees within 5 metres. We used Topographic Wetness Index (TWI, Beven & Kirkby, 1979), as a proxy for both the soil water available to the plant (Galiano et al., 2010) and soil depth and quality (Moore, Lewis, & Gallant, 1993). The TWI is a function of both the local slope and the upstream catchment area of a given point. We therefore computed TWI using the plot's local slope, previously captured in the field work, and the Digital Terrain Model (DTM) extracted from the Catalan Cartographic and Geologic Institution (ICGC).

2.4. Climatic Suitability Modelling and extrapolation to micro-local environment

Since *P. sylvestris* and *Q. pubescens* have a wide range of distribution and our study was focused on translating SDMs to micro-local conditions, we only considered occurrences in the Iberian Peninsula (N = 10,383 and 2,511, respectively). These occurrences were extracted from EU-Forest dataset (Mauri et al., 2017), which is based on almost 250,000 plots in the National Forest Inventories of most European countries. We excluded the southernmost occurrences in the Iberian Peninsula, which are considered a different infra-taxon (*P. sylvestris* var. *nevadensis*) (Olmedo-Cobo et al., 2017) that probably presents different niche characteristics due to local adaptations (Guisan et al., 2017).

We obtained SDM bioclimatic predictors from the CHELSA database version 2 (Fick & Hijmans, 2017) with a spatial resolution of 30'' (~0.7 km^2 at 40º N), based on climatic data from 1979-2013 period. To calibrate the model, we used the mean of six bioclimatic variables: annual mean temperature (Bio 1), mean temperature of the wettest quarter (Bio 8), mean temperature of the driest quarter (Bio 9), mean annual precipitation (Bio 12), precipitation seasonality (Bio 15) and precipitation in the wettest quarter (Bio 16). We selected these six variables following ecological criteria. Precipitation and temperature usually have an influence on the growth and survival of both *P. sylvestris* and *Q. pubescens* (Carlisle & Brown, 1968; Pasta, Rigo, Caudullo, & Commission, 2016). Summer precipitation and temperature during the winter are also relevant in *P. sylvestris* growth (Bogino et al., 2009; Misi, Puchałka, Pearson, Robertson, & Koprowski, 2019). Summer and winter correspond to the wettest and driest quarters, respectively, on our study site for the 1960-1990 climate period (Catalan Meteorological Station Network (Meteocat)).

The SDM algorithm used to calculate climatic suitability for both *Q. pubescens* and *P. sylvestris* was Boosted Regression Tree (BRT), applying the Gbm R package 2.1.3 (Ridgeway, 2007). We built SDMs following the standard criteria in the literature (Barbet-Massin et al., 2012; Elith et al., 2008; Pérez Navarro et al., 2018) and the calibration of the models was repeated three times using k-fold cross-validation with three different training and test datasets. The final models' output was based on all the occurrences. Model evaluations were based on the area under curve (AUC; Hanley and McNeil 1982) and on the variance explained, as R squared coefficient (see Table S2 of the supplementary material). These calculations were performed with the caret R package (Kuhn & others, 2008).

To capture the micro-local climatic environment, we generated our own bioclimatic variables (Bio 1, Bio 8 and Bio 9) using data-logger temperature records, which were captured directly for each tree location. Then, when extrapolating SDMs for each coordinate corresponding to the location of each studied tree we generated mean Climatic Suitability values for the studied period (2017-2019) by including the bioclimatic variables extracted from the data-loggers, instead of the CHELSA ones. Some data-loggers experienced occasional losses of data due to battery exhaustion or external incidents, such as animal interaction. To fill such gaps in the data, we built a Generalised Linear Model (GLM) to find the relationship between recorded climatic data in the plot and the climatic registrations in the three nearest plots. The model was then translated to those dates without data.

2.5. Statistical analyses

To test whether the effect of die-off on the canopy induced micro-local environmental changes along the altitudinal gradient, we built GLMs with the mean temperature of the driest quarter the mean temperature of the wettest quarter as the response variables and the elevation and type of plot (defoliated vs green canopy) as the explanatory variables. We also built a LM to elucidate whether Climatic Suitability varies across the altitudinal gradient for each species.

We also used one-way ANOVA to check whether plots with defoliated canopies had less canopy closure.

Two-way ANOVA with the HSD Tukey test was used to compare tree growth between the two studied species in the two different types of plots (defoliated vs green canopy). We used total Basal Area increment (BAI) during the three recorded years (2017, 2018, and 2019) as the response variable (tree growth). We preferred BAI to other variables such as radial increment because BAI is probably both more climate- and site-dependent (Pan, Tajchman, & Kochenderfer, 1997). Normality assumptions were tested using the Shapiro-Wilk test. To meet the assumptions of normality, BAI was log-transformed (Shapiro-Wilk test: $w = 0.98$, $p = 0.2252$).

Furthermore, GLMs were used to study the influence of micro-local variables on tree growth (BAI). We built two full models that included all the captured variables. First, we built a model (climatic suitability-based GLM) with TWI, BA, Hegyi index, canopy closure, species richness, plot type (defoliated vs green canopy), focal species (*Q. pubescens, P. sylvestris*), dbh and micro-local climatic suitability as explanatory variables. All the interactions between explanatory variables were introduced as well. Second, we built the same full model (climatic variables-based GLM), but using the three bioclimatic variables Bio1, Bio8 and Bio9 (annual mean temperature, mean temperature of the wettest quarter and mean temperature of the driest quarter, respectively) captured in the field, instead of the micro-local climatic suitability derived from SDM. The final models were selected according to a stepwise procedure based on the Akaike information criterion (AIC), using the MuMIn R package (Barton, 2018).

3. Results

3.1. Effect of canopy defoliation and elevation on species climatic suitability and micro-local climate

Pinus sylvestris and *Q. pubescens* showed significant differences in climatic suitability on our study site. Across all the altitudinal gradient, *Q. pubescens* has higher climatic suitability than *P. sylvestris* (Figure 2A, ANOVA, p <0.001, Table S2 of the supplementary material). Indeed, the climatic suitability for *P. sylvestris* increased with elevation, while the climatic suitability for *Q. pubescens* decreased (Figure 2A, Table S4 of the supplementary material).

Canopy defoliation had an effect on micro-local temperature, significantly increasing the temperature of the wettest quarter; this effect was consistent across the altitudinal gradient (Figure 2B, supplementary material Table S5).

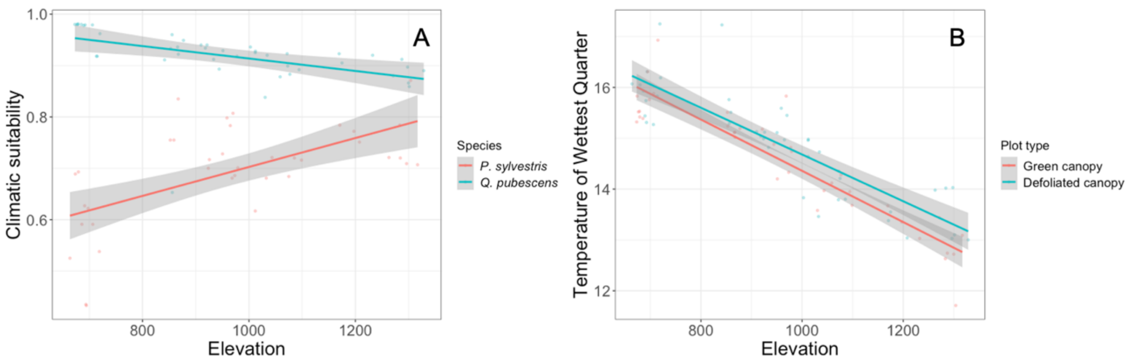

Figure 2. A: Relationship between species climatic suitability and elevation for *P. sylvestris* and *Q. pubescens* (differentiated by colour). B: Relationship between mean temperature of the wettest quarter (ºC) and elevation for green and defoliated canopies, showing higher temperature under defoliated canopy through the elevation gradient. Both relationships were obtained from the climatic suitability-based GLM.

3.2. Effect of canopy defoliation on the growth of sub-canopy trees

The BAI of the understorey trees was significantly higher under dead and defoliated canopy (Two-Way ANOVA: Sum. Sq =24.29, p < 0.001, Table S3 of the supplementary material). Although BAI was not significantly different between species overall (ANOVA; Sum sq. = 0.42, p = 0.303), the growth increase under defoliated canopy was different between *P.*

sylvestris and *Q. pubescens*, as supported by a significant interaction between the state of the canopy and the understorey species identity (ANOVA; Sum sq. = 4.14, $p = 0.002$. Accordingly, the increase on BAI between trees established beneath defoliated and green canopy was greater in *P. sylvestris* than in *Q. pubescens*. (Figure 3, Table S3). All the intra-specific comparisons between trees growing beneath green and defoliated canopies and all the inter-specific comparisons of trees growing beneath a given type of canopy were significant (Table S3).

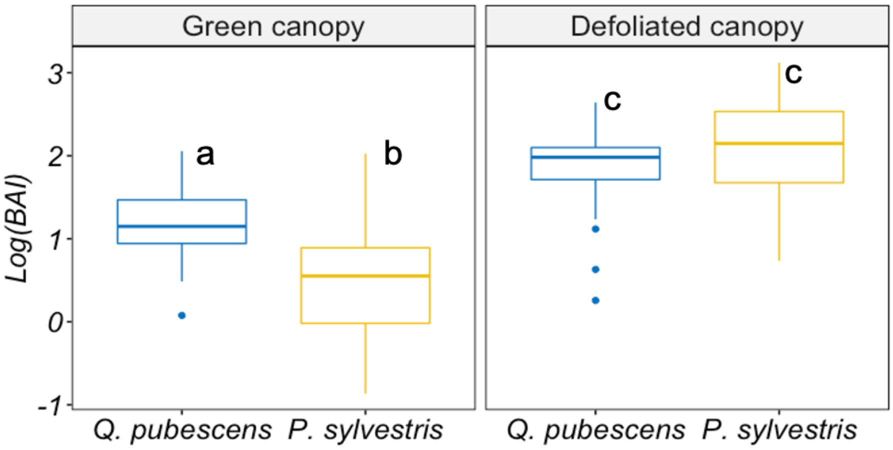

Figure 3: Boxplot panels indicating tree growth (log-transformed BAI) of understorey *Q. pubescens* and *P. sylvestris* individuals under green canopy (left panel) and defoliated canopy (right panel). Blue boxes represent *Q. pubescens* BAI and yellow boxes represent *P. sylvestris* BAI. The different letters indicate significant differences between species and type of canopy. The letters (a, b, c) indicate groups with significant differences according to the post-hoc Tukey test (supplementary material, Table S2).

Table 1: The results of the best-fitted climatic suitability-based GLM (first GLM) with BAI as response variable. The explanatory variables included in the model are: tree diameter, species identity (*Q. pubescens* or *P. sylvestris*), canopy closure and climatic suitability. Both interactions between species identity and canopy closure and climatic suitability were included. Variance explained as r2 are included in the last row.

	Estimate	Std. Error	p
Intercept	3.736435	0.594848	<0.00001
Diameter	0.053408	0.018145	0.00426
Species [Q. pubescens]	-3.259654	0.817032	0.000147
Canopy closure	-0.033207	0.003874	<0.00001
Climatic suitability	-1.500603	0.690677	0.032804
Species [Q. pubescens] * Canopy closure	0.018992	0.005113	0.000378
Species [Q. pubescens] * Climatic suitability	2.92263	1.059453	0.007209
			r^2 = 0.6492

3.3. Effect of environmental variables on the growth of sub-canopy trees

First, the best fitted climatic suitability-based GLM for BAI included tree diameter, canopy closure, species climatic suitability and species identity as the main factors, and the bivariate interactions between canopy closure and species climatic suitability with species identity (Table 1). The relationship between BAI and canopy closure and climatic suitability differed between species (Table 1, Figure 4A, 4B). Consistent with the previous Two-Way ANOVA, this model showed that *P. sylvestris* BAI increased more steeply with canopy defoliation than *Q. pubescens* BAI (Figure 4A). Also, *P. sylvestris* trees exhibited a higher BAI with decreasing climatic suitability. In the case of *Q. pubescens* the decrease of BAI with increasing climatic suitability is less pronounced (Table 1, Figure 4B) in comparison to *P. sylvestris*. Finally, BAI, overall, had a positively significant relationship with tree diameter (Table 1).

Table 2: Results of the best-fitted climatic variables-based GLM (second GLM) with BAI as response variable. The explanatory variables included in the model are: tree diameter, species identity (*Q. pubescens* or *P. sylvestris*), canopy closure and mean temperature in the wettest quarter. Both interactions between species identity and canopy closure and mean temperature in the wettest quarter were included. Variance explained as r^2 are included in the last row.

	Estimate	Standard error	p
Intercept	0.305629	1.392185	<0.00001
Diameter	0.060863	0.017457	0.000807
Species [Q. pubescens]	3.282667	2.043929	0.112303
Canopy closure	-0.03025	0.003863	<0.00001
Mean temp. of wettest quarter	0.110574	0.067343	0.104625
Species [Q. pubescens] * Canopy closure	0.016274	0.005033	0.001795
Species [Q. pubescens] * Mean TWQ	-0.217529	0.100216	0.033004
			r^2 = 0.6385

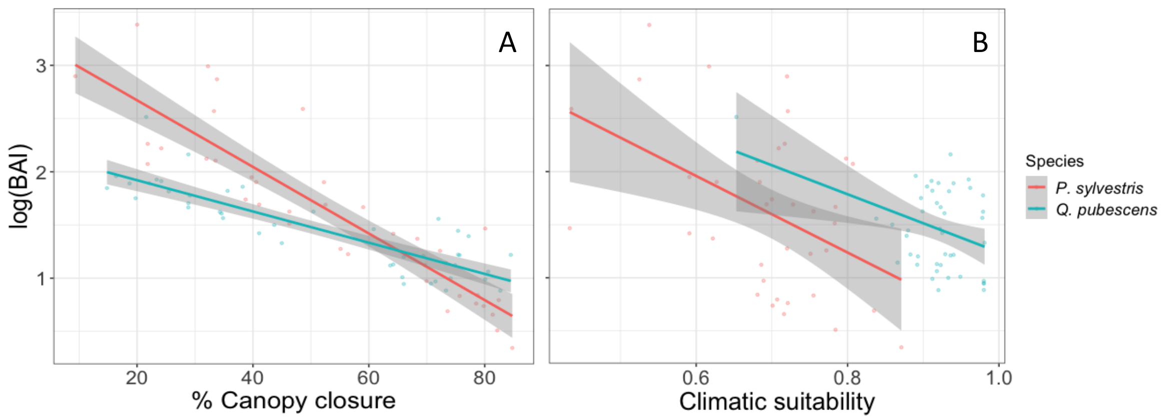

Figure 4: A: Relationship between predicted BAI and canopy closure (%) for *P. sylvestris* and *Q. pubescens*. B: Relationship between predicted BAI and climatic suitability. Both relationships were obtained from the climatic suitability-based GLM (First GLM).

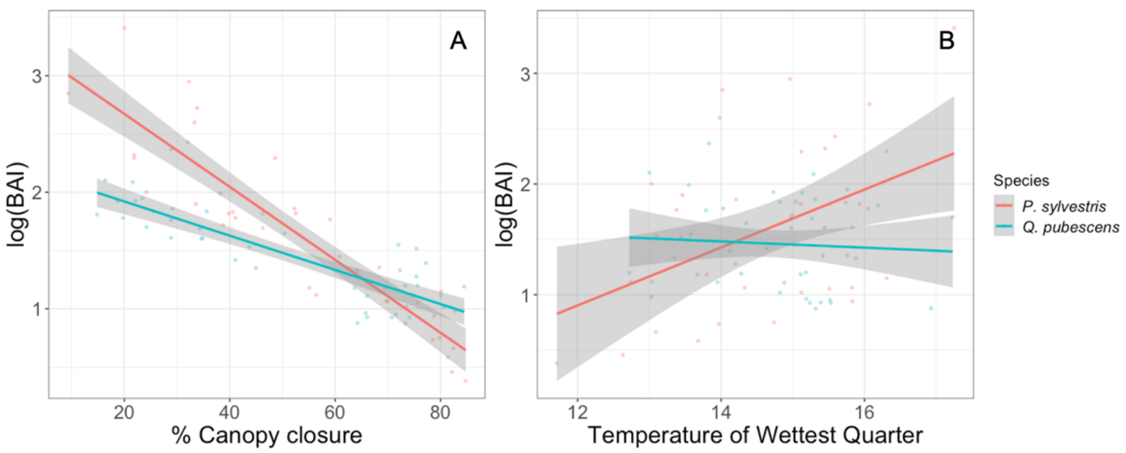

Figure 5: A: Relationship between predicted BAI and canopy closure (%) for *P. sylvestris* and *Q. pubescens*. B: Relationship between predicted BAI and Temperature of the Wettest Quarter. Both relationships were obtained from the climatic variables-based GLM (second GLM).

Second, the best fitted GLM using the micro-local measures of bioclimatic variables (climatic variables-based GLM) included the same independent variables as the climatic suitability-based GLM, but considering the mean temperature of the wettest quarter (TWQ) instead of climatic suitability (Table 2). This model showed that BAI significantly increased with higher mean temperature of the wettest quarter (from April to June) in *P. sylvestris*, but this effect was not observed in *Q. pubescens* (Table 2, Figure 5B). This model showed the same effect of tree diameter and canopy closure on the BAI of *Q. pubescens* and *P. sylvestris* than the climatic suitability-based model (Table 2, Figure 5B).

4. Discussion

4.1. *Pinus sylvestris* replacement

Both *P. sylvestris* and *Q. pubescens* showed increased growth under canopies affected by drought, but this increase was higher in *P. sylvestris*, supporting short-term self-replacement and the maintenance of *P. sylvestris* in the forest canopy. Canopy opening due to pine mortality or defoliation should favor the growth of species that require light, such as *Q. pubescens* and *P. sylvestris* (Diaci, Adamič, Rozman, Fidej, & Roženbergar, 2019; Pasta et al., 2016). However, *Q. pubescens* is more shade-tolerant than *P. sylvestris* (Niinemets & Valladares, 2006). Accordingly, in our forest *Q. pubescens* exhibited greater growth than *P. sylvestris* in sites with less canopy defoliation (more canopy closure). This agrees with previous observations that point *Quercus pubescens* as species with high survival rate during several years under denser canopies (Diaci et al., 2019). The gap that thus opens as a result of drought-induced pine mortality would represent a small-scale disturbance, pushing back community succession (Pulsford, Lindenmayer, & Driscoll, 2016) and favouring the pre-existing dominant *P. sylvestris*. Nevertheless, *Q. pubescens* trees also increased their growth on affected sites, indicating the potential of this species to achieve the forest canopy as a result of pine mortality, especially on sites where *P. sylvestris* individuals are not found in the understorey. Overall, these results are consistent with observations of both self-replacement and replacement of dominant species by other species following tree mortality events established in the understorey (Batllori et al., 2020, Lloret et al. 2021), and they illustrate the mechanisms involved in forest dynamics shortly after episodes of drought-induced mortality.

The species canopy replacement in drought-induced gaps will eventually be produced by the identity of trees established below or beside the affected canopy trees. This reinforces the idea that short-term replacement is more closely related to the presence of small trees rather than the abundance of seedlings on a given stand. In our studied forest, *P. sylvestris* seedlings and saplings are much more scarce than those of *Q. pubescens*, which may suggest on the long term an advantage of oaks over pines after the death of adult pines (Galiano et al., 2013). But seedling survival and growth can be extremely volatile and environmental and biotic dependent at small scales (Castro et al., 2004). Further, more developed juvenile stages of oaks in the understorey are rarer than in the case of pines, supporting the notion that the eventual short-term replacement of pines by oaks would be extremely local or patchy.

4.2. Influence of micro-local post-drought climatic conditions on tree growth

The temperature of the wettest quarter had a significant positive effect on tree growth, particularly in *P. sylvestris* individuals, suggesting that micro-local conditions modulate the growth of the remaining trees and, eventually, self-replacement after a disturbance (Elvira et al., 2021). Here, the wettest quarter of the year encompasses late spring (April to June, (Catalan Meteorological Station Network, Meteocat)), which coincides with the first part of the tree's growth season. Higher temperatures during the growing season can promote the growth of *P. sylvestris*, especially when the summer water deficit is low (Peltola et al., 2002). Moreover, other studies observed that when competition is low -like in drought-induced gaps- growth of the surviving trees is enhanced with higher temperatures, but these higher temperatures have a negative effect on growth in those plots with large basal area where competition is more intense (Wright, Sherriff, Miller, & Wilson, 2018). In addition, radiation is greater in these drought-induced gaps, thus creating drier and warmer conditions (Anderegg et al., 2012). An increase of temperature in the wettest quarter in defoliated plots was also observed on our study site (Figure 4B), and it could enhance the growth of *P. sylvestris* understorey trees, having less influence on the growth of *Q. pubescens*.

4.3. Climatic suitability indices derived from SDMs limitations

Overall, the climatic suitability inferred from SDMs did not consistently explain individual growth patterns. In fact, climatic suitability had a negative relationship with growth, particularly in *P. sylvestris* individuals (Table 1), suggesting that pine self-replacement could be faster in our study area in populations close to their tolerance limits. A poor relationship between *P. sylvestris* performance and climatic suitability indices derived from SDMs was also observed in resistance in French forests after the 2003 summer heatwave (Margalef-Marrase et al., 2020). In our area, greater climatic suitability was found at higher elevations, in agreement with the mountainous distribution of the Iberian *P. sylvestris* populations, which fed our SDM. Greater growth was observed, however, at lower elevation under warmer conditions, as seen by the positive relationship with the temperature of the wettest quarter (late spring). Overall, while the observed greater Scot pine growth at lower elevations can be explained by local milder climate, this local pattern would not be well captured by SDMs based on regional patterns of distribution. In the case of *Q. pubescens*, the expected higher growth trends induced by micro-local higher climatic suitability (Figure 4A, Table S2 of the supplementary material, Terradas et al., 2009) were neither supported by our BAI observations.

Although climatic suitability indices extracted from SDMs could be a tool to predict future vegetation shifts under climate-change scenarios (Kerns, Powell, Mellmann-Brown, Carnwath, & Kim, 2018) and explain patterns of drought-induced die-off effects (Lloret & Kitzberger, 2018; Pérez Navarro et al., 2018) or vulnerability to infestation by pests (Jaime et al., 2019), their relationships with vegetation dynamics (Thuiller et al., 2014) and growth trends (Dolos, Bauer, & Albrecht, 2015) are more elusive when micro-local environmental data are involved. Regional-scale models cannot capture relevant micro-local variability and, consequently, their scaling-down is not accurate enough, even when translating climate variables measured in the field. Moreover, the niche characterization across the different recruitment and replacement stages – from seedlings to adults – can differ (Canham & Murphy, 2017), since the growth and survival rates of the different life-history stages can be strongly dependent on biotic interactions (Miriti, 2006) and vary in terms of nutritional requirements (Bertrand et al., 2011). As a result, different life-history stages have a different relationship with climate, which is not fully captured in indices derived from SDMs. In contrast, micro-local measured climatic variables showed better performance and were more theoretically grounded when explaining individual patterns of tree growth. To summarize, regional-based indices such as climatic suitability can explain demographic processes, such as mortality and die-off effects, at equivalent spatial scales. These indices are difficult to translate to a more local scale, as they do not consider variables such as micro-climate, soil or biotic interactions, which operate at small spatial scale (Bertrand, Perez, & Gégout, 2012; Piedallu, Gégout, Lebourgeois, & Seynave, 2016). SDMs-based predictions of changes in both local growth and die-off trends can therefore be poor accurate, due to site-specific dependence (van der Maaten et al., 2017).

4.4. Future perspectives

The future climatic scenario in the region points to a rise in temperature of 2.2 ºC in 2050 compared to the period 1971-2000 (Calbó et al., 2016). Although precipitation is not expected to drop dramatically, these increasing temperatures are expected to raise water deficit (Calbó et al., 2016; Samaniego et al., 2018) and exacerbate the increase of extreme events such as droughts (Dai, 2013; Hari, Rakovec, Markonis, Hanel, & Kumar, 2020) and heatwaves in the coming decades (Viceto, Pereira, & Rocha, 2019). These extreme climatic episodes will probably lead to greater canopy defoliation and tree mortality in these rear-edge populations of

P. sylvestris, especially in stands with higher density and more competition (Bottero et al., 2017; Galiano et al., 2010). Herein, we report the ability of these populations to endure after such events, provided trees growing in the sub-canopy are available. Our findings also highlight the importance of stand structural features related to canopy closure in self-replacement. These features are closely linked to competitive processes, which, together other biotic interactions, make a significant contribution to the endurance of populations located close to its species' tolerance limits (Ettinger & HilleRisLambers, 2013). Accordingly, forest management in these populations should encourage the preservation of the tree understorey layer to ensure and accelerate the replacement of trees affected by die-off and eventual mortality, and thus guarantee trees' post-drought recovery (Aldea et al., 2017; Sohn, Saha, & Bauhus, 2016; Vila-Cabrera, Martinez-Vilalta, Vayreda, & Retana, 2011).

5. Conclusions

Short-term self-replacement patterns after drought-induced mortality in Pyrenean forests dominated by *P. sylvestris* were enhanced by micro-local conditions generated by the die-off itself, particularly temperature in the wettest quarter. Despite the low number of *P. sylvestris* seedlings available in the forest – in contrast with the high number of *Q. pubescens* seedlings and saplings (Galiano et al., 2010; Galiano et al., 2013)– a rapid replacement of dominant pines by oaks will probably not occur in the short term. Canopy recovery and replacement may be determined by trees growing in the understorey, where oaks are not so prevalent at the moment. Small-scale dynamics differences proved important, since while *P. sylvestris* can grow better than *Q. pubescens* in more opened gaps, *Q. pubescens* grows fast as pine under a healthy pine canopy. This difference in the performance of these two coexisting species makes it difficult to predict long-term future changes in rear-edge forests where species with different niches concur. This study highlights the importance of monitoring the different life-history stages (seedlings, saplings, understorey trees, adults) to predict future shifts in the community under climate-change scenarios. This study also provides evidence of mechanisms that promote the resilience of *P. sylvestris* forests meanwhile the tolerance limits of the species are not exceeded (García-Valdés, Estrada, Early, Lehsten, & Morin, 2020). But considering the climate-change context in which droughts are expected to be increasingly frequent, these mechanisms might finally collapse as well.

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