Species climatic niche and drought-induced forest dynamics

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Agraïments

El doctorat és la màxima distinció acadèmica que algú pot assolir i és fruit d'un llarg camí educatiu i vital que passa des de l'escola fins la formació no obligatòria universitària. Aquest, no és fàcil ni assequible per ningú, tanmateix jo he tingut un context familiar que m'ho ha posat molt fàcil. Per això voldria agrair a la meva família en especial als meus pares Cèlia i Ramon i a la meva germana Olga per proporcionar-me un ambient sa, feliç i ple d'inquietud científica. També voldria agrair a tots els professors tant de l'institut, grau i màster en els quals he pogut aprendre molt i han transformat la meva inquietud i curiositat en coneixement. Parlo d'en Delfí, Rafa, Joserra, Joan, Josep Antoni, Álvaro, Cristina entre altres; grans docents i persones amb les quals he aprés moltíssim tant a l'aula com al camp. La seva feina és de vital importància sobretot per a què estudiants de context diversos puguin arribar a la universitat i finalitzar aquests estudis amb èxit.

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Abstract

During the last decades forest die-off events have been reported in relation to climate-induced episodes, such as droughts and heat-waves. The causes of these phenomena have been extensively investigated from a physiological point of view. However, the consequences of the die-off process in terms of demography and forest dynamics have been less addressed. Regardless the expected relationship between climate and die-off, resilience of the affected populations and its associated post-disturbance dynamics cannot be described only considering regional climatic variables. It is also important to standardize the climatic conditions experienced by different populations during specific climatic events, considering the historic climatic conditions of the site where these populations live (bioclimatic niche). In this thesis SDMs derived indices are used for such purpose, thus investigating whether these indices can explain forest dynamics after drought events across different spatiotemporal scales.

In chapter 2, forest vulnerability during the extreme heat-wave occurred during 2003 was investigated at regional scale in France for fourteen species. SDMs indices were used to standardise the extreme climatic event conditions according to species climatic niche, as a tool to predict resistance to the heat-wave, estimated from remote sensing signal. Past climatic conditions and forest structure were also considered to evaluate forest resilience. Overall, forest resistance tended to increase in populations that historically have suffered high climatic variability. And it tended to decrease in populations that historically have lived in core-niche localities but have also experienced a reduction of suitability during the extreme event. Importantly, species-specific trends relating SDMs indices and stand structure to forest resistance emerged.

In chapter 3, the capacity of SDM derived indices to predict future forest dynamics after drought-induced forest die-off was investigated in several populations of *Pinus sylvestris* living in Catalonia. *P. sylvestris* plot dynamics considering young stages (seedlings and saplings)

were projected under different climate change scenarios to assess the resilience of this species populations after the die-off event. IPM methodologies -built from demographic vital rates- were applied to project plot structure at mid-term. Here, we used climatic suitability indices derived from SDMs to predict the performance of demographic vital rates. IPM projections indicate that full recovery will not be attained by 2069, although they suggest that post die-off recovery could be achieved later. Also, resilience capacity would diminish due to a reduction of climatic suitability induced by the increase of temperature in the expected climate change scenarios. These trends emerge from the balance between the loss of basal area during the drought event and the subsequent enhancement of tree recruitment.

In chapter 4, local self-replacement and replacement patterns in a rear-edge *P. sylvestris* population, placed in a forest with an altitudinal gradient and affected by drought-induced die-off was studied. SDMs derived indices from micro-local climatic data were tested to predict local canopy replacement of dominant *P. sylvestris* by another accompanying tree species (*Quercus pubescens)* with expected higher climatic suitability in this site. SDM indices failed to predict canopy replacement at this local scale. However, the micro-local conditions generated by die-off explained self-replacement across the altitudinal gradient.

This thesis demonstrates that SDMs derived indices are useful to standardise climatic extreme events at regional scale. Forest resilience to drought events across species and landscapes can be explained by historical conditions that populations have experienced (HCS, HCS-SD). Besides, forest structure influences populations' resilience at different spatiotemporal scales, being this influence more relevant at small scales. After drought-induced die-off events, recovery and self-replacement of previous dominant species can be attained by stabilizing mechanisms related to tree recruitment and growth, which in turn are driven by climatic suitability and by the new micro-local conditions generated by die-off events.

Resum

Durant les últimes dècades s'han observat una gran quantitat d'episodis de decaïment forestal relacionats amb fenòmens climàtics extrems, com ara sequeres i onades de calor. Les causes d'aquests fenòmens s'han investigat àmpliament des d'un punt de vista fisiològic. Tanmateix, les conseqüències del procés de decaïment pel que fa a la demografia i la dinàmica forestal han estat menys abordades. Tot i la relació esperada entre el clima i el decaïment forestal, la resiliència de les poblacions afectades i la seva dinàmica posterior a la pertorbació associada no es pot descriure únicament tenint en compte variables climàtiques regionals. Per entendre com aquests fenòmens climàtics extrems indueixen el decaïment forestal i com això afecta la seva dinàmica, és important estandarditzar les condicions climàtiques que experimenten les diferents poblacions durant un episodi concret, tenint en compte les condicions climàtiques històriques del lloc on aquestes poblacions hi viuen (nínxol bioclimàtic). En aquesta tesi hem utilitzat índexs derivats dels MDE (ICH, ICE, ICH-SD) com a eina per a aquest propòsit, i hem investigat si aquests índexs poden explicar la dinàmica forestal a diferents escala espaciotemporals.

Al capítol 2 es va investigar a escala regional i per a catorze espècies, la resiliència dels boscos durant una onada de calor que es va produir a França durant l'any 2003. Es varen utilitzar MDEs per estandarditzar les condicions durant l'episodi climàtic extrem en relació al nínxol climàtic de les espècies, com a eina per predir la resiliència de les poblacions. A més, es va avaluar si les condicions climàtiques passades i l'estructura forestal poden modular la resiliència forestal a escala regional. En general, s'ha observat que a escala regional la resistència dels boscos tendeix a augmentar en poblacions que històricament han patit una gran variabilitat climàtica i és més reduïda en aquelles poblacions que habiten la zona central del nínxol però que han experimentat un gran baixada de la idoneïtat climàtica durant el fenomen climàtic extrem.

Tanmateix han aparegut altres patrons de resistència específiques entre les diferents espècies estudiades.

Al capítol 3, es va investigar la capacitat dels índexs derivats dels MDEs per predir la dinàmica forestal futura després del decaïment induït per la sequera en diverses parcel·les de *Pinus sylvestris*. Es va projectar, sota diferents escenaris de canvi climàtic, la dinàmica de les poblacions de *P. sylvestris* per avaluar la resiliència després d'aquest esdeveniment de decaïment; considerant també les diferents etapes del regenerat. Es van utilitzar metodologies IPM -construïts a partir de taxes vitals demogràfiques- per projectar l'estructura de les parcel·les a mig termini, utilitzant índexs d'idoneïtat climàtica com a covariable. S’ha observat que la resiliència està relacionada amb els índexs d’idoneïtat climàtica derivats dels MDEs; i també, que la recuperació posterior al decaïment sembla ser possible a llarg termini. Però aquesta resiliència disminuiria a causa d'una reducció de la idoneïtat climàtica induïda per l'augment de la temperatura en els escenaris de canvi climàtic esperats.

Al capítol 4, es varen estudiar els patrons locals d'auto-reemplaçament i substitució en una població de *P. sylvestris*, situada en un bosc amb un fort gradient altitudinal i afectada per decaïment induït per sequera. Es va investigat si els índexs derivats dels MDEs mitjançant dades climàtiques micro-locals són útils per predir el reemplaçament de l’espècie dominant *P. sylvestris* per una altra espècie acompanyant (*Quercus pubescens*) amb una idoneïtat climàtica més alta en aquest bosc. Els índexs derivats dels MDEs no han predit el reemplaçament o auto-reemplaçament del dosser a escala local. No obstant això, les condicions micro-locals generades pel propi deccaïment sí expliquen l’auto-reemplaçament a través del gradient altitudinal.

Aquesta tesi demostra que els índexs derivats de MDEs són útils per estandarditzar els esdeveniments climàtics extrems a escala regional. També s’ha observat que la resiliència forestal entre espècies i paisatges es pot explicar amb les condicions històriques i passades que han experimentat les poblacions (ICH, ICH-SD). A més, l'estructura forestal influeix en la resiliència de les poblacions a diferents escales espaciotemporals; però la influència és més rellevant en petites escales d'estudi (capítol 3 i 4). També s’ha demostrat que després d'episodis de decaïment induït per sequeres, la recuperació i l’auto-reemplaçament de l’espècie prèviament afectada pot ocórrer mitjançant mecanismes d'estabilització, influenciats principalment per la idoneïtat climàtica i les condicions generades pel propi decaïment.

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Chapter 1

General introduction

1.1. Climate change and forest die-off

During the last decades the Earth is experiencing an accelerated global warming induced by anthropogenic activities involving CO_2 emission and land use changes, among others (IPCC, 2013). Consequently, this climate change is causing an increase in both frequency and intensity of extreme climatic events such as droughts, heatwaves, floods and windstorms (Lhotka, Kyselý, & Farda, 2018; Martinez-Alvarado et al., 2018; Seneviratne et al., 2012). Over the last years, a significant number of forest die-off and mortality episodes have been detected associated to these extreme events, specially to recurrent droughts, heat-waves or to a combination of both (Allen, Breshears, & McDowell, 2015; Allen et al., 2010; Carnicer et al., 2011; Clark et al., 2016).

The two main physiological hypotheses raised to explain tree mortality during these extreme events are related to hydraulic stress responses. They are identified as: (i) carbon starvation and (ii) hydraulic failure (Adams et al., 2009; Sevanto, Mcdowell, Dickman, Pangle, & Pockman, 2014). These two processes can also act coupled (Kono et al., 2019; Trifilò et al., 2017), and they even could be exacerbated by external conditions such as pests and pathogen infestation (Jactel et al., 2012). During a period of time with low soil water availability and high Vapor Pressure Deficit (VPD), plant can reduce canopy conductance, and save water by closing stomata (McDowell et al., 2008). Nevertheless, this process led the plant to avoid photosynthetic activity, and therefore, to diminish carbon assimilation, with the consequent reduction of the production of nonstructural and structural carbon compounds. If the hydraulic stress remains long enough, the reduction of canopy conductance drives the plant to die by carbon starvation (McDowell et al., 2008). This starvation is originated by a baseline oxidation of carbon compounds by respiration that can finally provoke the depletion of nonstructural carbon reserves (Galiano, Martínez-Vilalta, & Lloret, 2011; Sevanto et al., 2014). This process is particularly serious for Gymnosperms which are more prone to die by carbon starvation because they have smaller carbon reserves in comparison with Angiosperms (Adams, Zeppel, Anderegg, Hartmann, Landhäusser, Tissue, Huxman, Hudson, et al., 2017). However, if the plant strategy to face extreme drought is opening the stomata to avoid carbon starvation, the loss and use of water can provoke an embolism in the plant circulatory tissues. This originates an irreversible damage in the xylem and lead to the partial or total dead of the plant due to hydraulic failure and desiccation (Hartmann et al., 2018). Importantly, while most of the studies published to date have primarily addressed the physiological and environmental causes of forest die-off, only few studies have examined the consequences of this phenomenon at the level of vegetation dynamics (but see Batllori et al., 2020).

1.2. Vegetation dynamics

Vegetation dynamics comprises all the processes related to changes in plant community performances at different coupled spatial and temporal scales (Franklin et al., 2020; Hytteborn & Verwijst, 2011). In particular, vegetation dynamics includes the vegetation response at different time scales. On short time scales, encompasses physiological responses, such as carbohydrates dynamics (Dickman et al., 2015), and plant decay or mortality, which occurs from days to few years (Galiano et al., 2010; Lloret & Kitzberger, 2018; Pérez Navarro et al., 2018). At a medium time scales, comprises the changes in demographic and structural performances, such as seedlings dynamics or growth patterns that occur from years to decades (Kuuluvainen & Juntunen, 1998; Molowny-Horas, Suarez, & Lloret, 2017), and finally, at large temporal scales, ecological processes that can last from decades to centuries like succession and community and biomes shifts are considered. Simultaneously, the study of vegetation dynamics encompasses also different spatial scales, from individual to regional (Hytteborn & Verwijst, 2011). Likewise, we can consider the study of ecological processes at organism level, such as tree growth response under a given environmental condition or plant physiology response in front of stressors (H. D. Adams et al., 2013), the study at population and community level, that is, demographic and stand dynamics, which is usually relevant for management practices (Cobb et al., 2017), and finally the study at regional scale that involve landscape shifts, and changes in species and community distributions, which are relevant for global ecological trends including carbon and nutrient cycles (Kelly & Goulden, 2008; McDowell et al., 2016).

It is assumed that vegetation dynamics are clearly determined by the climatic conditions experienced by plants and communities in a given location. And also are related by other environmental variables such as those related to the pedosphere (Bauer, Mack, & Bever, 2015), or to biotic interactions, such as competition, facilitation and antagonisms, and human activities, such as management practices, and land use, operating across time (Wisdom et al., 2009). Historically, it has been considered that the community stability is reached under a constant climate, soil and land use (Clements, 1916). However, even when the environment is constant, the dynamics of vegetation can move on, reflecting changes of the community due to biotic interactions and time lags associated to different life histories, thus resulting in transformations of the environmental space by the stablished organisms (Pickett, Cadenasso, & Meiners, 2012). This process, known as ecological succession, is a sequency of phenomena that drives a plant community towards to late-successional stage - closer to the so-called climax communities (Margalef, 1977)-, which are characterized by high biomass accumulation and high complexity, but less productivity than the pioneer communities (Wang et al., 2004; West, Shugart, & Botkin, 1976).

The occurrence of disturbances, such as pest outbreaks, climate driven mortality events, wildfires, or windthrows, can provoke a regression of the ecological succession, thus pushing back the community again to a pioneer stage (Grime, 2001). Afterwards, rapid shifts to alternative states of the community determined by its composition, structure and functioning may occur as a result of the increase of frequency of those aforementioned disturbances (Millar & Stephenson, 2015; Nolan et al., 2021). This is particularly relevant when these disturbances are at some extent driven by climate, which is indeed changing. However, these changes in species composition and structure can push the community to another state which may be better adapted to the new climatic conditions, that is, showing more climate equilibrium with future conditions (Pérez-Navarro et al., 2021). Although these episodes of disturbances can potentially lead to important changes in forest communities, stabilizing mechanisms at populations and communities level, such as the presence of a seedbank, competition release and seedlings facilitation by the remaining trees or by the understory, can favor resilience against climate change induced disturbances (Gazol, Camarero, Vicente-Serrano, et al., 2018; Lloret, Escudero, Iriondo, Martínez-Vilalta, & Valladares, 2012; Redmond, Weisberg, Cobb, & Clifford, 2018). Therefore, the analysis of these mechanisms attains particular relevance in the current scenario of global change.

1.3. Community and ecological resilience

The capacity of populations and communities to persist, but also their performance across time against disturbances is called resilience, defined (by Tilman and Downing, 1994) as the ability to reach pre-disturbance performance levels. Resilience can be estimated by the ratio between the performance before and after the perturbation (Lloret, Keeling, & Sala, 2011). Two major components of resilience can be recognized: resistance and recovery (Ingrisch & Bahn, 2018). Resistance is defined as the ability to maintain system properties during a disturbance (Lepš, Osbornová-Kosinová, & Rejmánek, 1982), or in other words is the reversal of the reduction in ecological performance during the disturbance (Lloret et al., 2011). Individual and community resistance can be assessed by considering different properties of the system, such as individual growth (Colangelo et al., 2021), biomass accumulation (MacGillivray & Grime, 1995) or NDVI (Normalized Difference Vegetation Index) as a proxy of primary production (F. Lloret et al., 2007). Plant resistance has been explained by the species' specific nutrient stress tolerance (MacGillivray & Grime, 1995), plant functional traits and related physiological strategies (Vernon, Sherriff, van Mantgem, & Kane, 2018), stand characteristics and site quality (Lloret et al., 2007; Sánchez-Salguero et al., 2015) and also by taking into account the species characterization based on the ecoregion where they live and their related climate and geography (Hossain & Li, 2021).

On the other hand, recovery can drive the performance of the individuals (Gazol, Camarero, Sangüesa-Barreda, & Vicente-Serrano, 2018) or populations and communities to states similar to those before the disturbance (Peterson, Allen, & Holling, 1998). Thus, recovery is drove by different internal ecosystem processes that may occur after the disturbance such as both regeneration and further growth of the remaining individuals (Albrich et al., 2020). Then, community structural and individual features pushed towards those prior to the disturbance. Obviously, recovery is also determined by the environmental variability occurring after disturbances (Dobor et al., 2018; Zhu et al., 2020). But, other factors played an important role on recovery and resilience such as, past comunity structure, management and disturbance legacies and species richness (Seidl, Rammer, & Spies, 2014, Vogt et al., 2012).

Subsequently, the lesser is the ecosystem resistance, the higher recovery is needed to achieve similar resilience than ecosystems with high resistance. Therefore, an ecosystem with high resilience tends to show a high resistance or a high recovery and thus these two components could be at some extent complementary regardless the specific mechanisms influencing each of them (Ingrisch & Bahn, 2018; Lloret et al., 2011).

1.4. Species bioclimatic characterization

As we said before, there is a strong relationship between climate variables and forest die-off (Breshears et al., 2005; Goulden and Bales, 2019; Greenwood et al., 2017). Nevertheless the relationship between climate variable and tree decay and population die-off is not univocal (Hartmann et al., 2018). First, in the face of a specific climatic event, different species in a community may respond differently (Aguadé, Poyatos, Rosas, & Martínez-Vilalta, 2015; Pretzsch et al., 2020). And second, interactions between the different species of the community can modulated the severity of the disturbance (Pretzsch, Schütze, & Uhl, 2013; Svenning & Sandel, 2013). Also, in the face of the similar climatic event, different populations of the same species may respond differently, due to the existence of intraspecific variability promoted by acclimatization (Liu & Dickmann, 1993; Niinemets, 2010), local adaptations (Soliani, Mattera, Marchelli, Azpilicueta, & Dalla-Salda, 2021) or management legacies (Hereş et al., 2021). Finally, the intensity of a given climate extreme event can be variable at a regional scale, since weather is not constant across time and space, and it is usually modulated by the topography of the landscape (Clifford, Royer, Cobb, Breshears, & Ford, 2013).

Some authors have hypothesized that the species abundance tend to be greater at the center of the species geographical distribution and that they gradually decrease towards the geographic extremes of their distribution, thus reflecting the same pattern of species' fitness, and assuming a correspondence between the center of distribution and species optimum (Centre-Periphery CP hypothesis, see Sexton et al., 2009). Accordingly, populations located at the edges of the species geographical distribution will likely be more vulnerable to disturbances and climate change (Allen & Breshears, 1998). Therefore, these peripherical populations will be more easily replaceable by other coexisting species which will be located in its center of distribution (Martínez-Vilalta & Lloret, 2016). But, other studies have pointed out that the vulnerability to climate change may also be higher in the geographic center of distribution (Cavin & Jump, 2017). Overall, the CP hypotheses assumes the premise that there is a relationship between geographical space and climate, which is not always sustained (Pironon, Villellas, Morris, Doak, & García, 2015). Accordingly, the use of the climatic niche space to describe populations' performance instead geographic range may more accurate when studying communities' response in front of climate-induced disturbances. In this context, it is essential to establish a standardization for the adequacy of specific climatic conditions (e.g., past climatic conditions an future climate scenarios considering extreme episodes of drought) experienced by communities, in relation to the set of climatic conditions in which the species currently live, that is, its bioclimatic niche. This standardization would allow comparing (i) populations of the same species that have experienced different climatic regimes, and (ii) populations of different species that coexist and that experience the same climatic conditions. Such standardization of the climatic conditions that the populations experienced can be achieved by the characterization of the climatic space of the studied species, which would correspond to a subset of the species ecological niche.

1.5. Species Distribution Models and their use in vegetation dynamics

Basically, there exists two approaches to model the species ecological niche: climate envelope models, also known as correlative species distribution models (cSDMs), and process-based models, also known as mechanistic species distribution models (mSDMs). CSDMs allow to establish the relationships between environmental conditions (e.g., climate) and both presence and absence of the species occurrences (Jane Elith & Leathwick, 2009). These models are mainly based on species observations, so they basically describe the species' realized niche, that is, the environmental space where the species are found (Hutchinson, 1978). In contrast, mSDMs are based on physiological characteristics of the species, often incorporating in the model the relationship between functional traits and physiological and demographic performance to the environment. These SDMs are therefore more complex, but permit to build up the fundamental niche (Hutchinson, 1978): that is, the environmental space in which a given specie can persist (regardless biotic interactions, dispersion capacity, etc.). Accurate mSDM models are extremely difficult to build, especially when working with different species with complex life cycle, given the huge experimental setting needed. For these reasons, cSDMs are more often used than mSDM to construct species niche and particularly to predict species distributions. There are different cSDMs alghoritms usually used to build niche models, such as GLM, GAM, Random Forest or Maxent, among others (Franklin, 2010). All of them are based on species observations and absences or pseudoabsences. Therefore, the outputs of the models are the probability of appearance of the species in a given location, ranging from 0 to 1. This probability can be translated to less or more suitable climatic conditions for that species in a given place (Franklin, 2010). In other words, outputs of the cSDMs can be interpreted as the climatic suitability that experiences a given population in a given location, taking into account the whole species distribution and the climatic conditions in which it lives. In recent years, climatic suitability indices derived from SDMs have been used to characterize climatically populations –e.g., to check the Centre-Periphery hypothesis -, in relation to the vulnerability and resilience of populations in front of extreme climatic events (Lloret & Kitzberger, 2018) or biological disturbances such as pests (Jaime, Batllori, Margalef-Marrase, Pérez Navarro, & Lloret, 2019). Although these studies have documented how historical climatic conditions can explain the regional patterns of die-off in forest dominated by given species, less work was been done considering different species across space. Likewise, the relationship between suitability indices and resilience mechanisms such as growth or regeneration establishment are poorly understood (van der Maaten et al., 2017).

1.6. Thesis case study

During the last years, high climatic variability has resulted in a significant increase of high intensity of droughts and heat-waves across many biomes, including the temperate forests. Different droughts usually coupled with heat-waves (the so-called hot-droughts) have affected many temperate forests causing an increase of physiological stress in trees that can surpass their tolerance limits, eventually inducing die-off in several species, such as *Pinus sylvestris* (Bose et al., 2020), *Fagus sylvatica* (Leuschner, 2020), *Pinus halepensis* (Perez-Navarro et al., 2020), among others. One example of such events is the hot-drought that affected Western Europe during the 2003 (Rebetez, Mayer, & Dupont, 2006), which is considered to have been one of the most intense drought recorded before that date. Other episodes include the droughts of 2005 - 2006 (Jol, Raes, & Menne, 2009), 2012 (Camarero et al., 2018), 2018 - 2019 (Buras, Rammig, & S. Zang, 2020) that also induced forest die-off in the Iberian Peninsula and Western Europe (Banqué Casanovas, Vayreda Duran, & Martínez-Vilalta, 2013; Obladen et al., 2021; Senf, Buras, Zang, Rammig, & Seidl, 2020). Here I will use the 2003 hot-drought and 2012 droughts as study cases to evaluate how SDMs can capture the severity of such events and how they can be used to predict resilience and dynamics of the vegetation after the die-off events, across temporal and spatial scales.

1.7. Thesis aims

Extreme climatic phenomena, such as droughts, are increasing under climate change, and these events can affect vegetation dynamics. Ecological mechanisms determining resilience to such events can operate under the climate change context, but there still are uncertainties about when how they act, which prevent to determine the degree of resilience of different species to global change. Moreover, the relationship between extreme climatic events and vegetation responses are not clear enough when different spatiotemporal scales of observation are examined. In this sense, it is necessary to stablish methodologies that allow to explore at different scales - from trees to stands and landscape- how climatic conditions could affect vegetation dynamics. Here, I applied SDMs to standardize environmental conditions across scales and their relationships with vegetation dynamics. This rationale is particularly valuable when dealing with disturbances directly linked to climate, such as extreme drought, which result in forest die-off and eventual mortality.

The general aim of this thesis was to analyse and model plant and vegetation dynamics associated with climate change induced forest die-off across different spatiotemporal scales. For this purpose, we used climatic suitability extracted from species niche models (SDMs) as a tool to standardize climatic conditions experience by trees and forests and to explain the changes on vegetation dynamics induced by past and present climatic conditions. The specific objectives addressed in the different chapters were:

In chapter 2, the goal was to determine the existence of common patterns of population die-off vulnerability (i.e., lack of resistance) in front of climate extreme events at regional scale. For such propose we used the hot-drought event occurred across Western Europe during the 2003 summer as case study. We focused our study in pure forest populations of 14 different species across the French territory, where this episode was particularly intense. NDVI anomaly during a short period of time following the event was used as a tool to estimate the severity and the degree of affectation by drought. The historical climatic niche condition and its variability were characterized for each population. Also, standardization of the extreme event conditions according to species climatic niche was stablished and used as a tool to predict population vulnerability.

In chapter 3, the aim was to model forests dynamics of species populations affected by die-off, incorporating the climatic suitability for the population. We simulated at mid-term and under different climate scenarios the resilience capacity (engineering resilience) of populations affected by die-off, in comparison to unaffected populations. In this chapter, particular attention was given to the role of recruitment stages. For such purposes, demographic models inform on population performance over time, thus allowing to asses resilience after a given perturbation. In this sense, IPMs (Easterling, Ellner, & Dixon, 2000) allows great flexibility by integration functions describing the main processes (recruitment, growth, mortality) that determine stand structural features. These models were applied to *Pinus sylvestris* stands that experienced severe drought-induced die-off and mortality distributed across Catalonia to create simulations under climate change scenarios, which were run for more that 50 years, and they incorporated population's climatic suitability as a one of the predictors.

In chapter 4, the objective was to study local self-replacement and replacement patterns in a rear-edge *P. sylvestris* population affected by drought-induced die-off and mortality. In this forest, P. *sylvestris* and another accompanying species (*Quercus pubescens)* with different bioclimatic niche are distributed along a local environmental gradient, mostly determined by elevation. The aim was to investigate whether dominant *P. sylvestris* population affected by die-off are resilient after such perturbation, which create gap openings in the forest. We examinated if this new situation can promote replacement by *Q. pubescens*, which is expected to be experiencing more climatic suitability in that forest. Here, resilience was assessed by measures of individual growth, which were compared for the two coexisting species. This approach allowed us to predict future short-term canopy replacement and therefore, the degree of resilience. Further, climatic suitability of the coexisting species and other environmental variables (gap opening, micro-local temperature, elevation…) determining this feasible species replacement were analyzed.

Chapter 2

Relationship between heatwave-induced forest die-off and climatic suitability in multiple tree species

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Summary

In recent decades many forests die-off events have been reported in relation to climate change-induced episodes, such as droughts and heat waves. To understand how these extreme climatic events induce forest die-off it is important to find a tool to standardize the climatic conditions experienced by different populations during a specific climatic event, taking into account the historic climatic conditions of the site where these populations live (bioclimatic niche). In this study we used estimates of climatic suitability calculated from Species Distribution Models (SDMs) for such purpose. We studied forest die-off across France during the 2003 heatwave that affected Western Europe, by using 2,943 forest inventory plots dominated by fourteen single tree species. Die-off severity was estimated by NDVI loss using MODIS remote sensor imagery. Climatic suitability at local level during the historical 1979-2002 period (HCS), the episode time (2003) (ECS) and suitability variability during the historical period (HCS-SD)) were calculated for each species by means of BRT models using the CHELSA climate database and occurrences extracted from European forest inventories. Low HCS-SD and high mean annual temperature explained the overall regional pattern of vulnerability to die-off across different monospecific forests. The combination of high historical and low episode climatic suitability also contributed significantly to overall forest die-off. Furthermore, we observed different species-specific relationships between die-off vulnerability and climatic suitability: Sub-Mediterranean and Mediterranean species tended to be vulnerable in historically more suitable localities (high HCS); while, Euro-Siberian species presented greater vulnerability when the hot drought episode was more intense. We demonstrated that at regional scale, past climatic legacy plays an important role in explaining NDVI loss during the episode. Moreover, we demonstrated that SDMs-derived indexes, such as HCS, ECS and HCS-SD, could constitute a tool for standardizing the ways that populations and species experience climatic variability across time and space.

2.1. Introduction

Forest die-off and tree mortality events have been widely reported in recent years across many biomes, and they have been associated with hot drought episodes (Allen et al., 2015, 2010; Carnicer et al., 2011; van Mantgem et al., 2009) that can be related to climate change (IPCC, 2013). The evidence of the relationship between climatic variables (basically lack of precipitation combined with high temperatures) and forest die-off – loss of green coverage, leaf browning, growth reduction, partial dieback and even tree mortality- has mostly been observed at local scale for particular species (e.g., Faber-Langendoen and Tester 2006, Bigler et al. 2007, Sarris et al. 2007, Anderegg et al. 2011, Hereş et al. 2012). However, our understanding of the variability of forest die-off patterns at regional scale in relation to climate extremes, like hot-drought episodes, is still limited, particularly as regards comparisons of the performances of different species (Allen et al., 2015; Steinkamp & Hickler, 2015). Comparisons between species responses to similar climatic extremes across geographical gradients are challenging because of local environmental variability, including weather and soil variability (Adams, Barnard, & Loomis, 2014; Clifford, Royer, Cobb, Breshears, & Ford, 2013; Olarieta, Bargués Tobella, Rodríguez-Ochoa, & Antúnez, 2017; Western, Grayson, & Blöschl, 2002), population variability due to genetic, demographical and management legacy (Cavin & Jump, 2017; Hampe & Petit, 2005; Valladares et al., 2014; Vilà-Cabrera, Martínez-Vilalta, Vayreda, & Retana, 2011) and species attributes (Greenwood et al., 2017; Martinez-Vilalta, Lloret, & Breshears, 2012)

It is often assumed that species perform better when they are closer to their niche optimum rather than when they are near the edge of their niche (Abeli, Gentili, Mondoni, Orsenigo, & Rossi, 2014; Sexton et al., 2009). However, populations close to the centre of their species's climatic niche could be also affected by extreme climatic events (Lloret & Kitzberger, 2018) while, conversely, populations living under less suitable conditions could be less vulnerable

(Cavin & Jump, 2017; Lloret & Kitzberger, 2018). This pattern could appear as a consequence of high water-demanding organs, built during periods of high resource availability, of populations living close to climatic niche optimum or of local adaptation or phenotypic plasticity in niche edge populations (Rose, Leuschner, Köckemann, & Buschmann, 2009). However, these patterns could be modified by biotic interactions -i.e., competition, facilitation (Lloret & Granzow-de la Cerda, 2013)- or by increasing or decreasing vulnerability in the edge or core populations. More specifically, high stand density or high basal area has been reported as contributing to tree mortality under drought conditions (Bottero et al., 2017; Young et al., 2017).

Species distribution models (SDMs) are statistical models that relate species occurrences to environmental conditions, thus providing a species-specific index of habitat suitability, which can be specifically related to the climatic environment (species climatic suitability; Serra-Diaz et al., 2013). SDMs have been used to predict population demographic performance and species' persistence (Thuiller et al., 2014). Furthermore, SDMs have also been applied to standardize the climatic conditions undergone by different populations of a given species or different co-occurring species during the same extreme climatic event, relative to the historical climate conditions that each populations or species have experienced. (Sapes et al. 2017, Lloret and Kitzberger 2018, Perez et al. 2018).

Here we studied forest die-off during an extreme climatic event which occurred in France in 2003. From May to August 2003, vast areas of Western Europe experienced an extreme heatwave, concurrent with exceptionally low rainfall, and the functioning of forests was modified as a result (Ciais et al., 2005; Graf Pannatier et al., 2012; Pichler & Oberhuber, 2007). Thus, widespread forest die-off appeared in 2003 and their symptoms – i.e., loss of green canopy, leaf browning, growth reduction and mortality- remained in the following years (Allen et al., 2010; Bréda, Huc, Granier, & Dreyer, 2006; Lloret et al., 2007). This loss of green coverage resulted in an anomaly in the Normalized Difference Vegetation Index (NDVI) (Zaitchik, Macalady, Bonneau, & Smith, 2006).

The main goal of this study was to assess how climatic suitability during an extreme climatic event relates to die-off processes at regional scale, and to fourteen different forest tree species. We used several estimates of species climatic suitability derived from SDM outputs: Historical Climatic Suitability (HCS), which provided the suitability during the historical climate series; Event Climatic Suitability (ECS), which provided the suitability during the heat wave; and Historical Climatic Suitability Variability (HCS-SD), which provided the historical climate variability during the reference period (Lloret & Kitzberger, 2018). We also considered plot forest structure (density and basal area) as potential explanatory variable of die-off intensity (Klos et al., 2009; Linares, Camarero, & Carreira, 2010).

More specifically, we investigated (1) whether populations experiencing the hot-drought episode were highly affected when living close to their climatic limit of tolerance (negative effect of HCS on forest die-off) or when living close to the climatic optimum (positive effect of HCS on forest die-off), (2) the importance of extreme event magnitude on forest die-off (negative relationship between ECS and die-off), (3) whether populations were more affected in low climatic variability environments (negative effect of HCS-SD on forest die-off) or in high variability ones (positive effect of HCS-SD on forest die-off), thus demonstrating a climatic legacy effect in populations, (4) the interaction between climatic suitability variables in the elucidation of whether extreme episode suitability was increasing die-off close to the species' climatic optimum or close to their climatic limit of tolerance (interaction between ECS and HCS); and (5) whether past variability was reinforcing die-off in core or edge populations (interaction between HCS and HCS-SD) or whether climatic legacy events was reinforcing die-off in populations that experienced high drought magnitude (interaction between HCS-SD and ECS). Finally, we also tested (6) the importance of forest structure on forest die-off and whether forest structure modulates forest die-off in low or high climatic suitable populations (interaction between forest structure and Climatic Suitability Indices).

2.2. Methods

2.2.1. Study system

We performed the study in mainland France (3° 6' E, 42° 30' N to 2° 32' E, 51° 05' N, 334,604 km^2). During 2003 precipitation was lower than average from May to September -see figure S2 of the supplementary material-, especially in June and August (Rebetez et al., 2006). In particular, August rainfall was 20% to 75% lower than the average for that month in the 1961-1990 period. Furthermore temperatures in France were exceptionally high in 2003 (see figure 1b and figure S1 of the supplementary material), which came to be considered the hottest summer since 1500 (Luterbacher, Dietrich, Xoplaki, Grosjean, & Wanner, 2004). Maximum air temperature was higher than the 1961-1990 average for May (by 1-3ºC across the region) to August (by 4-6ºC) (Rebetez et al., 2006).

Our study was based on semi-natural woodlands as almost all European forests, which have been historically heavily managed and exploited (Farrell et al., 2000)- dominated by native species. We selected 6,400 plots from the French National Inventory (IFN) corresponding to the 2006 campaign. Since we aimed to analyze species-level patterns, we selected plots dominated by single species in order to minimize interactions between dominant species. We then selected those forest plots that satisfied the following requirements: (1) at least 40% of tree canopy cover; (2) location within a forest patch larger than 4 ha (200 meters of wide)); (3) dominant species that represented at least 67% of the total basal area. We then, chose 14 species that were dominant in at least 40 plots and selected the respective plots (see Table 1). Finally, we extracted the information relating to the total basal area (BA) and tree density (N) from each selected IFN plot. The final number of selected plots was 2,943 (Figure 1a, 1b).

2.2.2. Forest die-off maps

The Normalized Difference Vegetation Index (NDVI) (Tarpley, Schneider, & Money, 1984) was used to assess the vegetation response to the 2003 heatwave (Breshears et al., 2005; Lloret et al., 2007; Williams et al., 2013; Yuhas & Scuderi, 2009), since NDVI anomaly can be correlated to growth reduction (Kaufmann et al., 2008), loss of green coverage and warming-induced defoliation defoliation (Camarero, Franquesa, & Sangüesa-Barreda, 2015; Francisco Lloret et al., 2016) and eventual tree mortality (Breshears et al., 2005). All of these factors are symptoms of a die-off process (Jump et al., 2017).

NDVI images were extracted from the MODIS satellite after being calibrated and treated by the NASA/Goddard Space Flighter Center's Global Inventory Modelling and Mapping Studies (GIMMS) (source: http://glam1.gsfc.nasa.gov). The positive NDVI values of this database ranged between 0 and 250, and they had a spatial resolution of 0.0025 degrees and a time resolution of eight days; negative values –related to rock, snow and water -, were excluded. We linearly converted the NDVI pixels following MODIS specifications (source: *https://gimms.gsfc.nasa.gov/MODIS/README.txt*) - to a range of between 0 and 1. We used data from the Terra Modis products covering Metropolitan France from 2000 to 2003. We calculated the August NDVI mean for each pixel of the study area for the three years prior to the drought (2000, 2001 and 2002) and for 2003. In each pixel, we used the difference between the historical NDVI value and the 2003 NDVI value as a proxy of drought effects (Lloret et al., 2007) (Figure 1a), here basically die-off intensity –loss of green coverage or mortality-. NDVI can easily be affected by the timing of vegetation senescence, i. e., the yearly phenological cycle, and also by the specific composition of the plant cover (Soudani et al., 2012). Therefore, in order to avoid yearly NDVI dynamics, we excluded NDVI anomaly values for the autumn period, starting in September, after the hot drought episode, because in some deciduous tree populations leaf fall can begin in the early autumn months, potentially interfering with NDVI values Thus, we used the anomaly of a single month, in which the hot-drought episode ended (August), corresponding to the peak of the dry season, when herbaceous vegetation has probably decayed, causing minimal interference to the NDVI scores (Lloret et al., 2007). NDVI variability associated with species composition was minimized by considering pixels with a dominant forest species, virtually corresponding to monospecific stands, allowing for the analysis of species-specific responses. We used Terra Modis satellite imagery instead of other NDVI imagery sources with longer historical records because Terra Modis uses a resolution that correctly matches the studied forest patches in which the French inventory plots were located (0.0025 degrees at 46^o N longitude is equivalent to 200 m.).

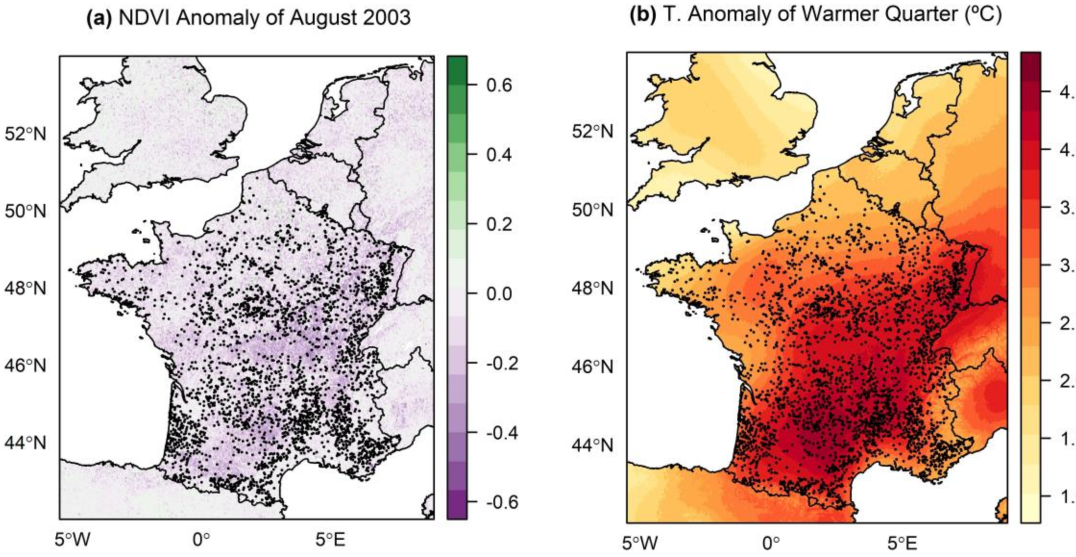

Figure 1: Map of the studied region (Metropolitan France) showing the August 2003 NDVI anomaly (a) (in absolute values, ranged from -1 to 1). Map of the studied region (Mainland France) showing the Temperature anomaly of the warmer quarter (b), in º Celsius. In both maps French Forest Inventory Plots of the fourteen studied species are represented as black dots.

2.2.3. Species Distribution Modelling (SDM)

We used SDMs of each studied specie to build species climatic suitability indices. The EU-Forest occurrence dataset (Mauri, Strona, & San-Miguel-Ayanz, 2017) was used to build SDMs for each studied species. This dataset of occurrences is based on almost 250.000 plots of National Forest Inventories of the main countries of Europe. The use of the EU-Forest dataset allowed us to include data on absence in our models, in contrast with other data sources, such as the Global Biodiversity Information Facility (GBIF), which only provide data on presence.

We obtained climatic data from the CHELSA climate world database (Karger et al., 2017), version 1.2, with 1 km^2 raster resolution for every year in the period 1979-2003. The raster layers of monthly precipitation and mean, maximum and minimum temperatures of this period were used to calculated 19 yearly standard bioclimatic variable raster files (Table S2, supplementary material), using the dismo R package (Hijmans, Phillips, Leathwick, & Elith, 2011). To calibrate the model, we used the mean of the six least correlated bioclimatic variables in all the EU-Forest occurrences, for the 1979-2002 reference period (isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, precipitation seasonality and precipitation of wettest quarter), after testing the collinearity between the nineteen explored bioclimatic variables by means the Variation Inflation Factor (VIF) (Marquaridt 1970).

SDM algorithm used to calculate species' climatic suitability was Boosted Regression Tree (BRT) using the Gbm package 2.1.3 (Ridgeway, 2007). General Additive Models (GAM), GLM and BRT built with bioclimatic variables can have highly correlated outputs (Pérez Navarro et al., 2018), and among them BRT is recognized as the best in terms of accuracy and adjustment (Jane Elith & Graham, 2009). Nevertheless, we also ran GAM algorithm since them are recognized to better characterize response curves' smoothness (Elith, Leathwick, & Hastie, 2008), in order to ensure BRT prediction robustness and to identify possible prediction errors. Finally BRT showed better performance in terms of AUC (Area Under receiver operating characteristic Curve, Hanley and McNeil 1982) and higher explained variance (See supplementary material, Table S1).

We built the species distribution model following recommendations from the literature: number of real absences equivalent to the number of species occurrences by randomly choosing from the total absences (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Pérez Navarro et al., 2018); tree complexity of 5 for those species with more than 250 occurrences and of 3 for those species with less than 250 occurrences. The learning rate of 0.005 was chosen because it made it possible to achieve at least 1,000 trees in each case (Elith et al., 2008).

The calibration of the model was repeated three times using k-fold cross-validation with three different training and test datasets. Model evaluation and final model output were based on the average of the three models (Pearson et al., 2006; Thuiller et al., 2004). The evaluation of the final models was based on the area under curve (AUC; Hanley and McNeil 1982) and variance explained as R squared coefficient (see Table S1 of the supplementary material), using "caret R package" (Kuhn & others, 2008).

Each built SDM was projected to the average historical conditions (1979-2002) of each selected French Forest Inventory plot in order to calculate the HCS of each plot. SDMs were also projected on to each single year of the 1979-2002 period. We then, we calculated the standard deviations of these projections (HCS-SD) in order to estimate the variability of the species climatic suitability on each plot of the French Forest Inventory (Lloret & Kitzberger, 2018). We also projected each species' model on to the 2003 climatic conditions found on each plot to obtain the event climatic suitability (ECS), which shows the degree of unfavourability of climatic conditions during a particular moment (Lloret & Kitzberger, 2018; Pérez Navarro et al., 2018).

2.2.4. Die-off modelling

First, we built a generalized mixed model (GLMM) with normal distribution for assess the general relationship between forest die-off and climatic suitability. We used the lme4 R package (Bates, Mächler, Bolker, & Walker, 2015), in which we included mean August NDVI loss as a dependent variable. The independent variables in the model were climatic suitability estimators (ECS, HCS, HCS-SD), the bivariate interactions between these bioclimatic variables and two climatic variables (Mean Annual Temperature (T) and Mean Annual Precipitation (P)) as fixed effects, and species as a random effect. We included these climatic variables to test whether populations distributed in warmer or wetter regions were more or less affected during the climatic event. Moreover, we included the interaction of T and P with HCS in order to analyse which edge of the climatic range were more affected during the extreme event (i.e., the wettest or the driest, or the warmest or the coldest edge). Each replicate was a French National Inventory plot. The final model was selected according to stepwise procedure based on the Akaike Information Criterion (AIC), using the MuMIn R package (Barton, 2018).

Table 1: Species description, including leaf seasonality, chorological distribution, and number of French National Inventory plots used in the GLM.

Specie	Vernacular Name	Family	Leaf seasonality	Chorology	Plots
Abies alba	Silver fir	*Pinaceae*	Evergreen	Euro-Siberian	185
Betula pendula	Silver birch	*Betulaceae*	Deciduous	Euro-Siberian	44
Castanea sativa	Sweet chestnut	*Fagaceae*	Deciduous	Sub-Mediterranean	171
Fagus sylvatica	European beech	*Fagaceae*	Deciduous	Euro-Siberian	334
Fraxinus excelsior	European ash	*Oleaceae*	Deciduous	Euro-Siberian	63
Picea abies	Norway spruce	*Pinaceae*	Evergreen	Boreo-Alpine	201
Pinus halepensis	Aleppo pine	*Pinaceae*	Evergreen	Mediterranean	67
Pinus nigra	Austrian pine	*Pinaceae*	Evergreen	Sub-Mediterranean	51
Pinus pinaster	Maritime pine	*Pinaceae*	Evergreen	Sub-Mediterranean	274
Pinus sylvestris	Scots pine	*Pinaceae*	Evergreen	Euro-Siberian	287
Quercus ilex	Holm oak	*Fagaceae*	Evergreen	Mediterranean	95
Quercus petraea	Sessile oak	*Fagaceae*	Deciduous	Euro-Siberian	457
Quercus pubescens	Downy oak	*Fagaceae*	Marcescent	Sub-Mediterranean	291
Quercus robur	Common oak	*Fagaceae*	Deciduous	Euro-Siberian	423

Second, for each species we used a Generalized Linear Model (GLM) with normal distribution to evaluate the relationship between forest die-off (estimated as a NDVI loss) and climatic suitability estimators (HCS, ECS, HCS-SD) and forest structure (BA, tree density). We made species-specific modelling to increase the sensitivity of the models since the species could have different distributions patterns and the significant variables across models may be different. All possible bivariate interactions were also included in the models. Longitude and latitude coordinates were also incorporated to take into account geographical trends and to elucidate whether die-off vulnerability increases in specie's northern or southern distributions limits. The final models were selected according to stepwise procedure based on the Akaike Information Criterion (AIC), using the MuMIn R package (Barton, 2018). The significance of the drop in climatic suitability between historical conditions (HCS) and event climatic conditions (ECS) were tested by the Kruskal–Wallis test (Kruskal & Wallis, 1952). All the statistical analyses were carried out with the R version 3.4.0 (R Core Team 2017).

2.3. Results

2.3.1. General analysis of forest die-off

The best fitted model, according to AIC, was a GLMM built with HCS-SD, mean annual temperature (T), mean annual precipitation (P), HCS, ECS and the following interactions: HCS:ECS, HCS:T and HCS:P. There was a negative relationship between both HCS-SD and mean annual temperature and forest die-off (Figure 2a, Table 2). Meanwhile, HCS:ECS emerged as a significant negative interaction (Figure 2b).

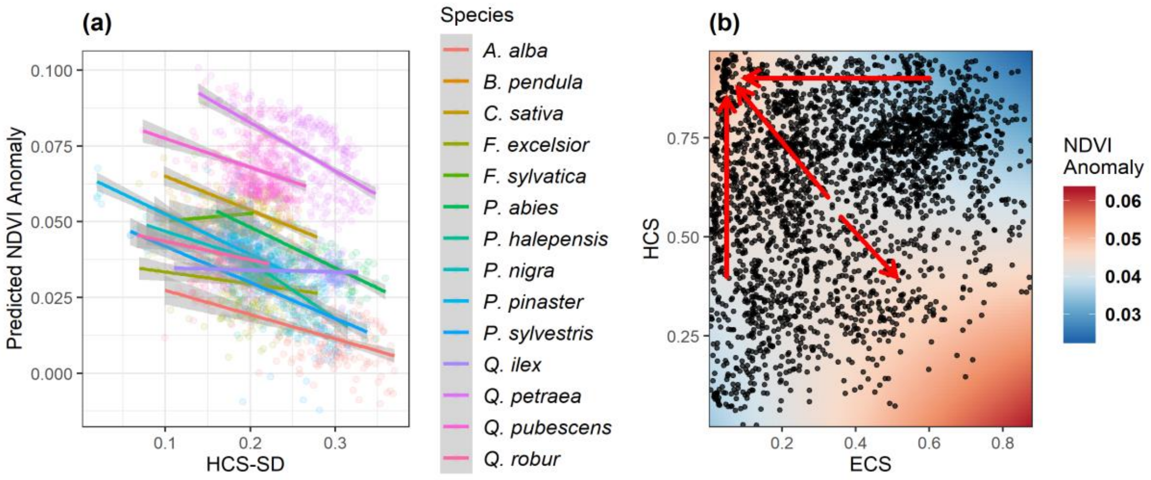

Figure 2: HCS-SD effect on NDVI loss according to GLMM considering all species right (a). Die-off at different combination of HCS and ECS during the 2003 summer (reader colour means more die-off likelihood) (b). Dots indicate the situation of inventory plots in the bivariate space determined by ECS and HCS. Arrows are indicative of the direction of the HCS:ECS interaction; they approximately correspond to the higher slope with high density of plots.

Table 2: Results of GLMM considering all species ans plots (N=2,943), with NDVI loss (August 2003) as dependent variable and ECS, HCS-SD, HCS, T and P as explanatory variables.

r^2 = 0.09	***Estimate***	***P value***
Intercept	-0.0420	0.2429
HCS	0.0576	0.2815
ECS	0.0327	0.0748
HCS-SD	-0.1042	0.0016
HCS:ECS	-0.0665	0.0133
Temperature	0.0076	0.0003
Precipitation	0.00001	0.5053
HCS:T	-0.0039	0.1883
HCS:P	0.000004	0.8768

2.3.2. Species-specific die-off analyses

At species level, we found significant correspondences between die-off (NDVI loss) and some of the climatic suitability indices and plot structure variables in twelve of the fourteen studied species. We failed to obtain any significant bioclimatic or structural predictor in the *Pinus sylvestris* and *Picea abies* models (Table 3).

Table 3: Results of final GLMs for the different forest species, considering NDVI loss (August 2003) as dependent variable and SDM outputs (ECS, HCS, HCS-SD), stem density (N), basal area (BA), UTM X and Y coordinates as explicative variables. Interactions between variables are also included.

	Abies alba		***Betula pendula***		***Fagus sylvatica***		***Quercus robur***	
	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*
Intercept	0.0249	0.591	1.5966	<0.0001	0.2410	0.0013	0.6306	<0.0001
ECS	-0.2874	0.015	-4.7574	0.0241	-0.2990	0.0236	-0.2210	0.0119
HCS-SD	-0.0421	0.772	-9.8489	<0.0001	-0.1392	0.4734	0.1193	0.4297
N	1.31e-05	0.0865	-	-	1.18e-05	0.0258	-	-
ECS:HCS-SD	0.8548	0.029	30.7873	<0.0001	1.2040	0.0433	-	-
ECS:BA	-	-	0.0263	0.0243	0.0024	0.0373	-	-
BA	-	-	-0.0096	0.0241	-0.0008	0.0819	0.0004	0.1406
X	-	-	-	-	-0.0027	0.0403	0.0017	0.3634
Y	-	-	-	-	-0.0036	0.0193	-0.0119	<0.0001
HCS	-	-	-	-	-	-	-0.0666	0.1967
HCS:ECS	-	-	-	-	-	-	0.3350	0.0141
r^2	*0.07*		*0.38*		*0.10*		*0.08*	

HCS was positively related to NDVI loss –greater die-off- in plots dominated by *Pinus nigra*, *Pinus pinaster*, *Quercus ilex* and *Castanea sativa* (Table 3). Lower ECS values were significantly related to greater die-off in plots dominated by *Abies alba*, *Betula pendula, Fagus sylvatica* and *Quercus robur* (Table 3). We found a positive interaction between HCS and ECS in plots dominated by *Q. robur* (Table 3) showing that the positive influence of HCS on die-off was greater in populations with high ECS (Figure 3). In contrast, in plots dominated by *P. nigra*, a significant negative interaction between HCS and ECS was found (Table 3); it was determined by higher die-off with a combined effect of high HCS and low ECS (Figure 3). In plots dominated by *P. pinaster, Pinus halepensis, Quercus pubescens* and *B. pendula,* lower HCS-SD was significantly related to greater die-off. Conversely, in plots dominated by *Q. ilex* and *C. sativa*, higher HCS-SD was significantly related to greater die-off (Table 3). In these plots, HCS-SD also showed a significant negative interaction with HCS (Table 3), due in *Q. ilex* to greater die-off with low HCS and high HCS-SD values, and in *C. sativa* to more die-off in plots with low HCS-SD and high HCS (Figure 3c, 3i). Finally, there was a positive interaction between ECS and HCS-SD in *A. alba*, *B. pendula* and *F. sylvatica* (Table 3), with greater die-off in plots with a high variability of past climatic suitability, even in conditions of mild unsuitable conditions during the episode (high ECS); in the case of *B. pendula* this vulnerability also occurs in plots with low climatic variability that experienced low values of ECS (Figure 3).

Table 3. Extended.

	Castanea sativa		*Pinus nigra*		*Quercus ilex*		*Pinus pinaster*		*Quercus pubescens*	
	Estimate	Pr (>t)	Estimate	Pr (>t)	Estimate	Pr (>t)	Estimate	Pr (>t)	Estimate	Pr (>t)
Intercept	-0.2636	0.0303	0.0014	0.9646	- 0.3441	0.0221	0.0693	0.0891	0.3200	0.0022
HCS-SD	1.5603	0.0120	-	-	1.8399	0.0047	-0.5447	0.0137	-0.9991	0.0347
HCS	0.5799	0.0015	0.1226	0.0497	0.4833	0.0216	0.1302	0.0102	-0.1926	0.1097
BA	0.0005	0.1354	-	-	-0.0005	0.0286	-0.0005	0.6951	-	-
N	-	-	3.06e-05	0.2403	-	-	-	-	-	-
ECS	-0.0599	0.0927	0.1378	0.1189	-	-	0.0341	0.0922	0.1496	0.1689
HCS:HCS-SD	-2.8319	0.0010	-	-	-2.4586	0.0054	-	-	-0.7149	0.0779
X	-	-	-	-	0.0034	0.0174	-	-	-	-
ECS:N	-	-	-7.89e-05	0.0928	-	-	-	-	-	-
ECS:HCS	-	-	-0.3909	0.0316	-	-	-	-	0.8679	0.1056
HCS:BA	-	-	-	-	-	-	- 0.0034	0.0198	-	-
HCS-SD:BA	-	-	-	-	-	-	0.0122	0.0724	-	-
r^2	0.12		0.24		0.23		0.09		0.14	

We observed a positive effect of tree density on the NDVI loss in plots dominated by *Fraxinus excelsior* and *Quercus petraea*. In contrast, in plots dominated by *B. pendula* and *Q. ilex*, basal area was negatively related to forest die-off (Table 3). In two of these species (*F. excelsior* and *Q. petraea*), only plot structure variables exhibited any significant effect on NDVI loss (Table 3).

Table 3. Extended.

	Pinus sylvestris		*Picea abies*		*Fraxinus excelsior*		*Quercus petraea*		*Pinus halpensis*	
	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*
Intercept	0.4019	0.0002	0.0310	<0.0001	0.0341	0.0104	0.5397	<0.0001	0.1611	0.0158
N	-	-	2.28e-06	0.6930	3.00e-06	0.0429	0.0005	0.0264	-	-
BA	-	-	-	-	-	-	1.28e-5	0.1096	-	-
HCS-SD	0.0834	0.2611	-	-	-	-	-	-	-0.5498	0.0378
X	-	-	-	-	-	-	0.0026	0.0538	-	-
Y	-	-	-0.0085	0.0003	-	-	-0.0107	<0.0001	-	-
HCS	-	-	-	-	-	-	-	-	-0.1397	0.1411
HCS:SD-HCS	-	-	-	-	-	-	-	-	0.6057	0.0768
r^2	0.05		0.06		0.07		0.08		0.07	

We also found some significant interactions between structural parameters and bioclimatic variables. We found a positive interaction between ECS and basal area in plots dominated by *B. pendula* and *F. sylvatica* (Table 2). In these cases, the die-off was greater with the combination of a low basal area and low ECS (Figure 3d, 3e). In plots dominated by *P. pinaster* there was a negative interaction between HCS and BA, indicating a greater die-off under combined low HCS and a high basal area (Figure 3i).

Latitude and longitude (Y and X coordinates) were not significant in most of the species models. Otherwise, we observed a negative relationship between latitude and loss of NDVI in *F. sylvatica, Q. robur, Q. petraea, P. abies* and *P. halepensis* (Table 3), supporting a higher die-off in the southern limit of species distribution.

2.4. Discussion

2.4.1. General trends of forest die-off resistance during the heat-wave

The combination of climatic suitability derived from SDMs (HCS, ECS and HCS-SD) and mean annual temperature was able to partially explain regional die-off patterns across monospecific forests during the 2003 heatwave in Europe. This agrees with other studies that have used SDM to explain the effect of historical climatic conditions (Lloret and Kitzberger 2018, Perez Navarro et al. 2018), loss of climatic suitability (Lloret & Kitzberger, 2018; Sapes et al., 2017) or the past stability of climatic conditions (Lloret & Kitzberger, 2018) on forest die-off vulnerability at local and regional scales. Climatic Suitability during the extreme hot-drought (ECS) decreased in all cases respect to historical climatic suitability (HCS) except for *P. sylvestris* (Table S1, SM I).

These results demonstrate that climatic variables associated with water deficit play an important role in forest die-off across a regional scale, as in other studies (e.g.. Clifford et al. 2013, Lloret and Kitzberger 2018). They also support the hypothesis that SDM outputs could be used as a tool for standardizing the magnitude of a given extreme climatic event to explain vegetation responses across geographical gradients.

Historical climatic variability (HCS-SD) and the interaction of HCS and ECS proved to be significant for explaining forest die-off across species. Mean annual temperature also has a positive significant effect on forest die-off, showing that populations living under warmer conditions and species with warmer distributions could be more vulnerable to the episode. This warm-edge vulnerability is not directly related to the vulnerability of populations living near their limit of tolerance since no interaction was found between HCS and Temperature. From this general viewpoint, the variability in historic climatic suitability emerged as a relevant variable to explain forest die-off, demonstrating that plots with more historic stable conditions

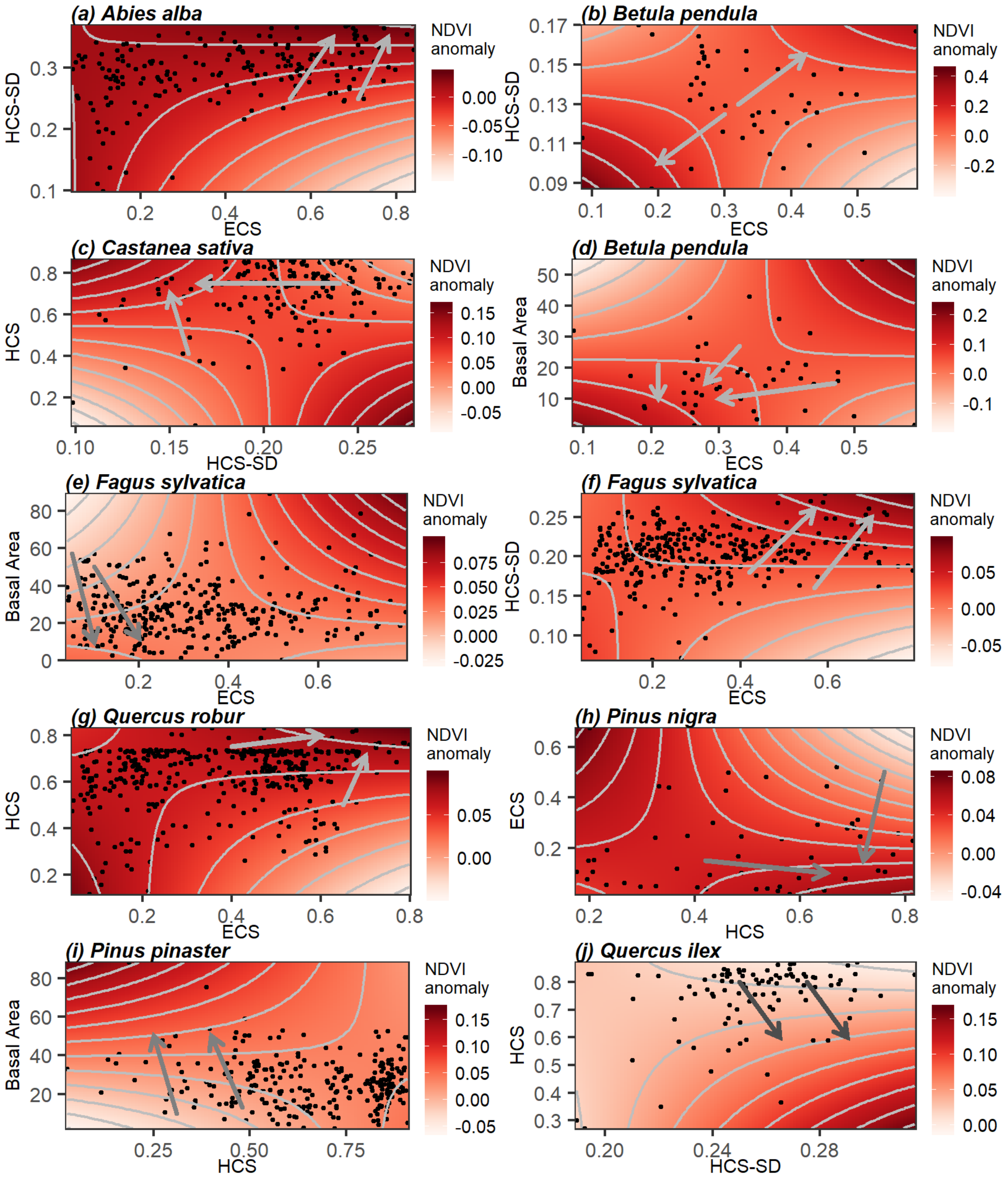

Figure 3: Interactions between explanatory variables (SDM outputs and basal area) obtained in GLMs of different species, illustrated by contour graphs of the 2003 summer loss. Redder surfaces indicate more NDVI loss and dots indicate the situation of French inventory plots in the variables space. Arrows are indicative of the direction of the interaction; they correspond to the higher slope with high density of plots. The graphs were obtained after fitting the GLM for each species (see Material and methods).

showed more die-off in the face of a sudden pulse of variability, corresponding to extreme water deficit conditions. Interestingly, we also documented higher vulnerability to die-off in populations that experienced a greater magnitude of the episode when located in historically high suitable conditions, indicating that even populations living under regular suitable climatic conditions may be vulnerable to extreme pulses of climate variability, such as heat waves and droughts (Lloret & Kitzberger, 2018). So, acclimatization to past suitable conditions should increase vulnerability to extreme climatic episodes (Clark et al., 2016). Alternatively, the combinations of low HCS and high ECS (low magnitude of the episode) also tended to induce die-off, also highlighting the vulnerability of populations living at the edge of their climatic envelope when experiencing just a mild pulse of climatic adversity. From these general trends, species-specific patterns emerged elsewhere.

2.4.2. Species specific patterns of forest die-off resistance

In four Euro-Siberian species, typical of wet, temperate to moderately cold climates *(A. alba, B. pendula*, *F. sylvatica* and *Q. robur)*, die-off was specially explained by low ECS values, revealing the vulnerability of species used to living in moist conditions when confronting episodic extreme hot and drought conditions. This result agrees with other studies that have reported sensitivity of these species to high levels of drought and temperature (Castagneri, Nola, Motta, & Carrer, 2014; Cavin & Jump, 2017; Kharuk, Ranson, Oskorbin, Im, & Dvinskaya, 2013; Linares & Camarero, 2012). Indeed, species with high water demand tend to be less drought-resistant, especially in moist and damper sites (Clark et al., 2016). This vulnerability could be related to ecological traits such as high-leaf area, low wood density (Greenwood et al., 2017) and poor hydraulic performance (P50) (William R. L. Anderegg et al., 2016).

Interestingly, Sub-Mediterranean species such as *P. pinaster*, *P. nigra*, *C. sativa* and the Mediterranean *Q. ilex* exhibited greater die-off in populations that have historically experienced better climatic conditions (higher HCS). In the case of *P. nigra*, this trend was exacerbated by the combination with higher stressing conditions during the event (low ECS). In *P. pinaster* populations, the trend was enhanced by low variability in historical climatic conditions (low HCS-SD), suggesting an acclimatization to suitable regular conditions. Several hypotheses can explain the vulnerability of populations living under constant conditions closer to species's climate optimum: (1) populations located in mesic sites may develop high leaf area and high basal area due to acclimation, which makes them especially vulnerable to a large drop in moisture availability (Clark et al., 2016; Jump et al., 2017); (2) populations located in climatically unsuitable areas usually live in sites where micro-local conditions such as soil characteristics and topography can buffer the effect of climatic anomalies at larger spatial scales (Lévesque, Rigling, Bugmann, Weber, & Brang, 2014); (3) populations from less suitable regions may have developed local adaptations enhancing resistance to more stressful climate (Rose et al., 2009).

Other species (*A. alba*, *B. pendula*, *F. sylvatica*, *P. halepensis*, *Q. petraea*, *Q. pubescens*) do not show any clear pattern of vulnerability in relation to the historical climatic suitability of the sites where their populations live. In fact, in these species, populations living near their tolerance limits or under very suitable conditions were equally prone to die-off during the extreme climatic event. Vulnerability to extreme episodes would probably be derived from processes operating at population level. In addition to local climatic conditions, historical legacies, such as management practices (Vilà-Cabrera et al., 2011), colonization history, genetic background (Valladares et al., 2014) and topographic and soil conditions (Galiano, Martínez-Vilalta, & Lloret, 2010; Lloret, Siscart, & Dalmases, 2004) have been reported as being important modulators of vulnerability to die-off.

2.4.3. Climatic variability and forest die-off

We found a significant negative relationship between HCS-SD and green canopy loss across species at a regional scale (Table 2, Figure 2a). The mechanism involved in this vulnerability could be related to an acclimatization process under relatively stable conditions that provokes a great dependence on a regular water supply (Clark et al., 2016). This also implies that populations of those species living in highly variable climatic environments (high HCS-SD) are less vulnerable to die-off, maybe due to local adaptation to high climatic variability (Valladares et al., 2014). This pattern is visible in different species such as *B. pendula, P. halepensis*, *P. pinaster* and *Q. pubescens*. Furthermore, higher stable conditions (low HCS-SD) reinforce the vulnerability to die-off near the climatic optima or during the event, as seen in populations of *C. sativa* and *B. pendula* (Figure 3).

In contrast, in populations of *Q. ilex*, die-off was enhanced by greater HCS-SD and low HCS, suggesting the existence of mechanisms of the so-called legacy effect involving cumulative damage, such as xylem embolism and carbon reserves depletions (Waldboth & Oberhuber, 2009). More specifically, the inability to recover carbon reserves after recurrent suitability changes can be higher in populations located in historically poor suitable conditions (Lloret et al., 2018). Vulnerability to die-off due to legacy effect also occurred in populations of *A. alba*, *F. sylvatica* and *B. pendula* that experienced mild drought during the episode (low ECS) (Figure 3). These results support the hypothesis that previous extreme droughts could increase vulnerability to die-off, even in highly resilient species like *Q. ilex* (Galiano, Martínez-Vilalta, Sabaté, & Lloret, 2012; Lloret et al., 2004) or during non-extreme drought episodes. However, the lack of a positive relationship between historical climatic variability and die-off in many species suggests that vulnerability to drought due to this legacy effect probably persists for only a few years after a drought episode, since the recovery of carbon reserves and new tissues can be quite fast (Galiano et al., 2012).

2.4.4. Forest structure and die-off resistance

In accordance with other studies (Bottero et al., 2017; Galiano et al., 2010; Jump et al., 2017; Vilà-Cabrera, Martínez-Vilalta, Galiano, & Retana, 2013), we also observed a positive significant correspondence between green canopy loss and plot density in species such as *F. excelsior* and *Q. petraea* (Table 3). This relationship is explained by greater competition for water in denser plots (Bottero et al., 2017). In the case of *P. pinaster*, a high basal area increased vulnerability in those plots that historically experienced poor suitable conditions (Figure 3), i.e., those that were likely more water-limited (Clark et al., 2016; Young et al., 2017).

Conversely, basal area or plot density did not enhance forest die-off in other species. Furthermore on *Q. ilex,* and *B. pendula* plots, die-off was greater on plots with a low basal area. In fact, a low basal area would represent less competition, but it may also indicate a site with poor-quality habitat. So, sites that are less suitable due to low soil quality (e.g., rocky or thinner soils) could maintain a lower basal area (Meyer, North, Gray, & Zald, 2007) while being particularly vulnerable to episodic water deficit. Accordingly, the positive interaction between basal area and ECS observed in *B. pendula* and *F. sylvatica* plots would indicate that vulnerability to die-off from strong drought in these species was greater on plots located in poor suitable conditions. Finally, die-off intensity in *P. abies* and *P. sylvestris* across all the regional gradient was not explained by either bioclimatic or structural variables, although some local studies have shown the contribution of forest structure to drought-induced die-off in *P. sylvestris* (Galiano et al., 2010; Rigling et al., 2013; Vilà-Cabrera et al., 2013).

2.4.5. SDM derived indices limitations

Apart from species-specific responses to climate across the region, the absence of this relationship may reflect some limitations in SDMs when characterizing the suitability of a tree population since they generally disregard intra-specific genetic variability, phenotypic plasticity, biotic interactions, dispersal constraints or past management (Franklin et al., 2013). They also assume that species' response to bioclimatic variables is homogenous across all the species' range (Benito Garzón, Alía, Robson, & Zavala, 2011). *Pinus sylvestris*, with a wide range of distribution and high intra-specific genetic variability (Matías & Jump, 2012; Rehfeldt et al., 2002), could be poorly characterized with the use of SDM, especially if local adaptions and genetic plasticity are not considered (Benito Garzón et al., 2011). Meanwhile, the distribution of *P. abies* has been substantially modified by management practices (Hansen & Spiecker, 2005) and their SDMs could be skewed by, for instance, artificial plantations that could be installed in unsuitable locations.

2.5. Conclusions

Nevertheless, this study shows that SDM outputs interpreted as climatic suitability indices are related to climate-induced forest die-off following certain extreme climatic events across regional scales. This approach may not be so effective to explain patterns of tree growth over longer periods of time as climatic variability may be buffered over the life span of long-living species (van der Maaten et al., 2017). More specifically, our results show that ECS is a useful index for standardizing the magnitude of extreme climatic events and enabling comparisons across landscapes for distinct forest species. The use of SDMs also makes it possible to evaluate interactions between past and present climatic conditions and thus assess the existence of reinforcing effects and the vulnerability of niche-core and niche-edge populations. We also demonstrated that, although vulnerability to die-off is species-specific, some trends related to species' chorology can be found (i.e., Euro-Siberian vs. Mediterranean and Sub-Mediterranean species). However, our study focused on monospecific populations, so further research applying this methodology to mixed forests is required to scale up the use of climatic suitability indices to community level.

Acknowledgements

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Supplementary Material Chapter

Table S1: Description, evaluation and mean outputs of the climatic suitability models built for the studied forest species. In each case the model description includes: number of occurrences (N), model evaluation (AUC),), explained variance of the model (r^2), mean HCS of the inventory plots (HCS), mean ECS of the inventory plots (ECS), the significance of the difference between HCS and ECS during the hot-drought event using *Kruskal-Wallis* Test (K-W test) and mean HCS-SD of the inventory plots. SD is also provided after mean values.

Species	***N***	***AUC BRT***	***r^2 BRT***	***AUC GAM***	***r^2 GAM***	***HCS***	***ECS***	***K-W test***	***HCS-SD***
Abies alba	3,127	0.94	0.626	0.80	0.308	0.743± 0.221	0.404± 0.228	< 0.0001	0.292±0.048
Betula pendula	6,794	0.86	0.359	0.69	0.217	0.397±0.097	0.331±0.100	0.0001	0.134±0.020
Castanea sativa	3,016	0.92	0.533	0.89	0.246	0.702±0.144	0.193±0.149	< 0.0001	0.211±0.034
Fraxinus excelsior	5933	0.87	0.384	0.77	0.214	0.481±0.159	0.273±0.141	< 0.0001	0.166±0.021
Fagus sylvatica	11,937	0.99	0.455	0.83	0.263	0.572±0.190	0.319±0.179	< 0.0001	0.203±0.032
Picea abies	23,307	0.93	0.551	0.85	0.450	0.619±0.152	0.513±0.261	0.0008	0.244±0.056
Pinus halepensis	4,359	0.98	0.810	0.98	0.565	0.786±0.195	0.172±0.133	< 0.0001	0.298±0.039
Pinus nigra	3,550	0.93	0.536	0.85	0.311	0.500±0.190	0.203±0.162	< 0.0001	0.156±0.032
Pinus pinaster	5,490	0.95	0.617	0.96	0.397	0.657±0.195	0.225±0.162	< 0.0001	0.259±0.046
Pinus sylvestris	25,031	0.87	0.396	0.83	0.283	0.274±0.106	0.275±0.164	0.7575	0.162±0.025
Quercus ilex	7,549	0.95	0.623	0.96	0.401	0.745±0.126	0.472±0.232	< 0.0001	0.255±0.024
Quercus petraea	5,704	0.91	0.488	0.85	0.327	0.702±0.135	0.564±0.149	< 0.0001	0.196±0.030
Quercus pubescens	2,840	0.96	0.706	0,93	0.359	0.841±0.144	0.300±0.240	< 0.0001	0.265±0.044
Quercus robur	10,322	0.89	0.446	0,83	0.244	0.629±0.130	0.396±0.191	< 0.0001	0.209±0.028

Table S1 extended: Relative influence of each variable used to build the BRT model for each specie.

Species	***Bio 3***	***Bio 4***	***Bio 8***	***Bio 9***	***Bio 15***	***Bio 16***
Abies alba	19.54	20.99	5.58	22.14	5.73	26.00
Betula pendula	37.53	18.62	6.25	12.64	18.61	6.33
Castanea sativa	11.17	17.03	13.65	24.42	18.19	15.53
Fraxinus excelsior	16.59	17.05	11.26	26.28	23.95	4.87
Fagus sylvatica	33.35	19.81	4.66	17.29	16.92	7.97
Picea abies	8.50	25.60	6.13	47.49	7.50	4.78
Pinus halepensis	3.34	4.73	8.54	11.96	57.44	13.91
Pinus nigra	22.71	16.69	11.67	25.02	17.81	6.08
Pinus pinaster	9.63	8.28	6.50	53.51	13.24	53.51
Pinus sylvestris	44.69	14.69	8.15	19.65	5.49	7.33
Quercus ilex	11.83	7.18	5.48	9.66	57.94	7.90
Quercus petraea	36.23	19.66	5.40	15.53	17.67	5.49
Quercus pubescens	23.76	22.78	5.56	17.49	26.41	3.99
Quercus robur	6.65	18.53	15.73	28.12	24.45	6.51

Table S2: Bioclimatic variables generated to build the SDM. Finally, only the 6 less correlated were used (Bio 3, Bio 4, Bio 8, Bio 9, Bio 15 and Bio 16; See material and methods)

Bioclimatic variables	
Annual Mean Temperature	Bio 1
Mean Diurnal Range	Bio 2
Isothermality (Diurnal range/Annual range)	Bio 3
Temperature Seasonality (Temp. SD · 100)	Bio 4
Maximum Temperature of Warmest Month	Bio 5
MinImum Temperature of Coldest Month	Bio 6
Temperature Annual Range	Bio 7
Mean Temperature of Wettest Quarter	Bio 8
Mean Temperature of Driest Quarter	Bio 9
Mean Temperature of Warmest Quarter	Bio 10
Mean Temperature of Coldest Quarter	Bio 11
Annual Precipitation	Bio 12
Precipitation of Wettest Month	Bio 13
Precipitation of Driest Month	Bio 14
Precipitation Seasonality (Coefficient of Variation)	Bio 15
Precipitation of Wettest Quarter	Bio 16
Precipitation of Driest Quarter	Bio 17
Precipitation of Warmest Quarter	Bio 18
Precipitation of Coldest Quarter	Bio 19

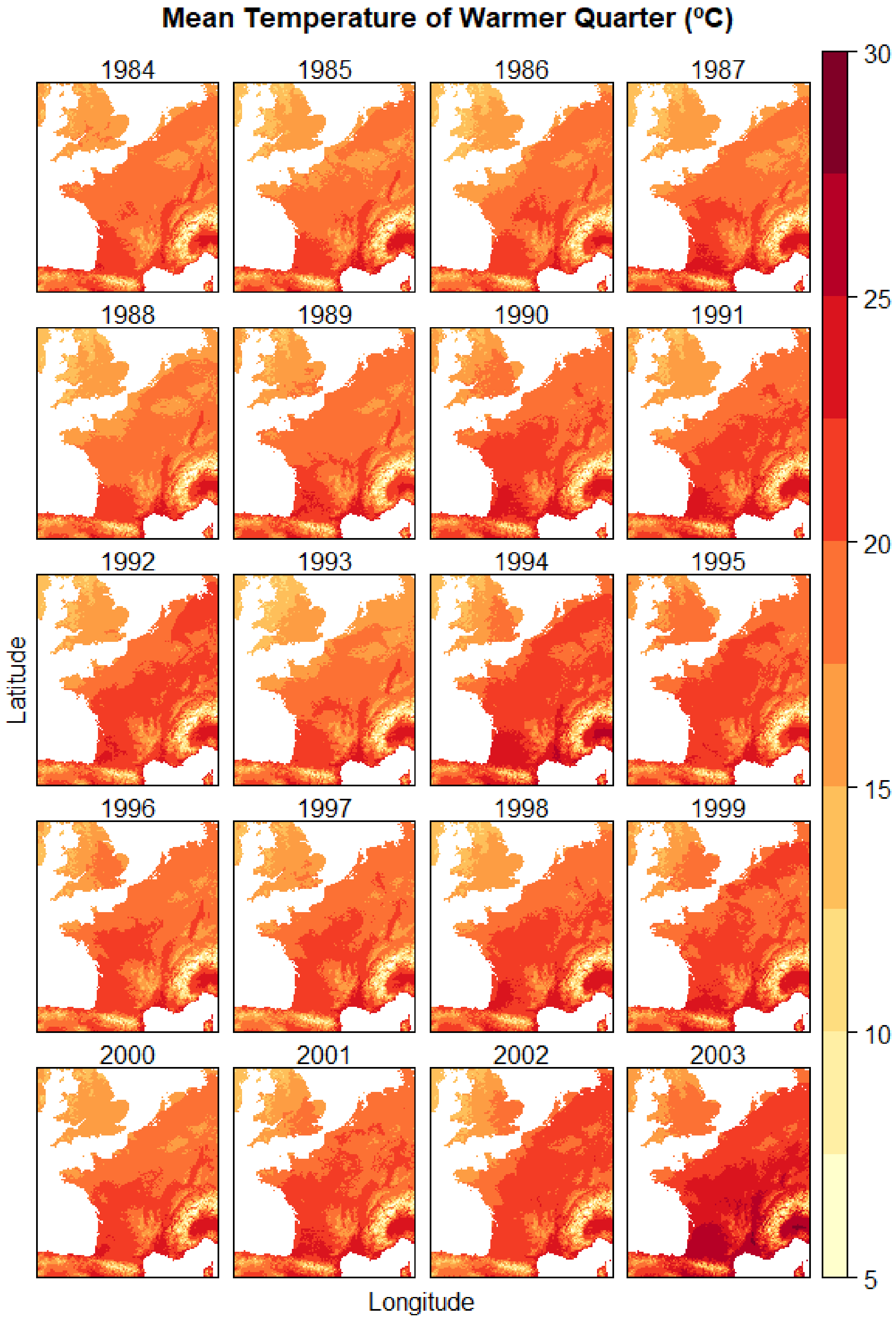

Figure S1: Time series (1984-2003) of the mean temperature of the warmest quarter (Bio 10). Source: CHELSA database.

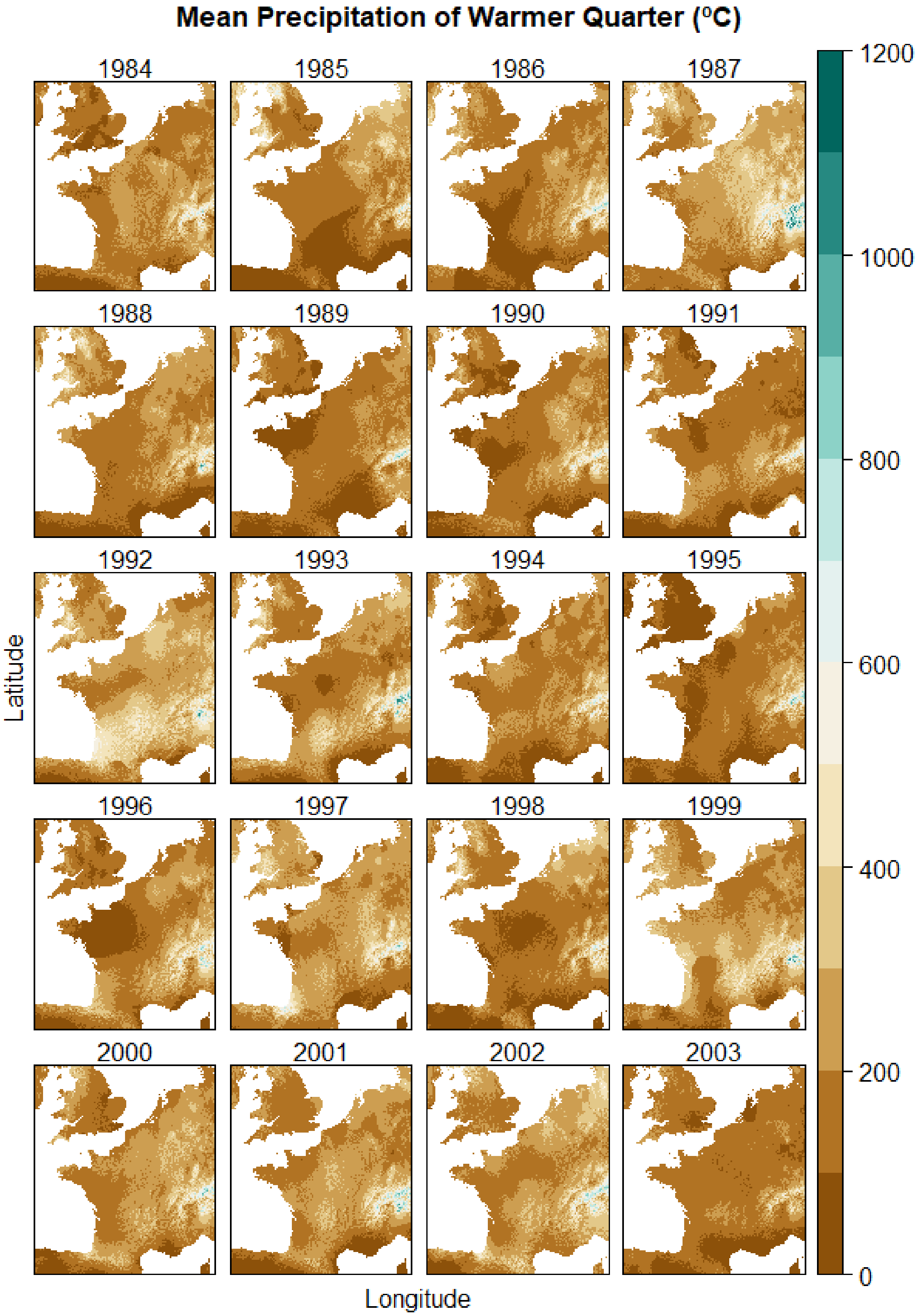

Figure S2: Time series (1984-2003) of the precipitation of the warmest quarter (Bio 18). Source: CHELSA database

Chapter 3

Modelling the dynamics of *Pinus sylvestris* forests after die-off event under climate change scenarios

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Summary

During the last decades, die-off events in *Pinus sylvestris* populations are on the rise, usually related to local and regional extreme hot droughts. The causes of these phenomena have been extensively investigated from a physiological point of view. However, the consequences of the die-off process in terms of demography and vegetation dynamics have been less addressed. Here, we projected under climate change scenarios *P. sylvestris* plot dynamics after a die-off event, considering also the young stages (i.e., seedlings, saplings and ingrowth from the sapling to the adult class), to assess the resilience of *P. sylvestris* populations after such event. We used IPM methodologies to project future plot structure under three climate scenarios (current climate, RCP4.5 and RCP8.0 projections) using climatic suitability -extracted from Species Distribution Models- as a covariable in the vital rates through time. Field data feeding IPM were obtained from two successive surveys, starting at the end of the die-off event (2013) and four years later (2017), carried on populations sited across the *P. sylvestris* range of distribution in Catalonia (NE Spain). Plots affected by die-off experienced a loss of large trees which determines that plot basal area, tree diameter and tree density will remain, during decades, lower that non-afected plots in these plots. This situation is counterbalanced at some extent in affected plots by higher basal area increment and seedling recruitment into the tree stage after the event, thus promoting resilience. However, resilience is delayed under the climate change scenarios with warmer and drier conditions involving additional physiological stress. This delay was due to a reduction of seedling abundance and lower plot basal area. Overall, the study shows the lagged effect of drought-induced die-off events on forest structure and reveals stabilizing mechanisms, such as recruitment and tree growth release, which enhance resilience. These mechanisms, however, appears jeopardized by warming in the region.

3.1. Introduction

Forest die-off is currently occurring across most biomes, and the consequences of the phenomenon are raising major concern, particularly under climate change conditions (Allen et al., 2015; Anderegg et al., 2015; Clark et al., 2016). The association of this phenomenon to climate change is supported by the observed relationship between local climatic variables (particularly the lack of precipitation combined with high temperatures) with green coverage loss, leaf browning and tree mortality (Allen et al., 2010; Greenwood et al., 2017; Williams et al., 2013b), although other agents, such as insects and pathogens, can also intervene (Jaime et al., 2021; Wong & Daniels, 2017). The forest die-off often occur concurrently with extreme climatic events –i.e. droughts (Senf et al., 2020) and heat-waves (Margalef-Marrase, Pérez-Navarro, & Lloret, 2020)- associated with the increase of climatic variability that accompanies climate change. The environmental and physiological mechanisms that ultimately cause tree mortality have been extensively studied (Adams, Zeppel, Anderegg, Hartmann, Landhäusser, Tissue, Huxman, McDowell, et al., 2017a; McDowell et al., 2018; Nathan G. McDowell & Allen, 2015), revealing the importance of the interaction between hydraulic failure and carbon starvation, particularly in conifer species (Adams, Zeppel, Anderegg, Hartmann, Landhäusser, Tissue, Huxman, McDowell, et al., 2017). However, the understanding of the recovery of structural and compositional forest characteristics following these die-off events remains limited (but see Martínez-Vilalta and Lloret 2016, Batllori et al. 2020). Especially, the contribution of juvenile stages to this recovery and its integration together with tree mortality and growth rates (Clark et al. 2016) has not yet been sufficiently addressed.

The studies that have analysed the resilience in terms of resistance and recovery of tree populations to climate-induced die-off have revealed the importance of the role of historical climatic conditions, which can be estimated from climatic suitability indices derived from Species Distribution Models (Lloret & Kitzberger, 2018; Margalef-Marrase et al., 2020). For instance, regarding resistance, events of forest die-off can especially affect those populations living under low suitable historical climatic conditions, i.e., located at the edge of their range of distribution, that is at their tolerance limit (bioclimatic niche edge) (Camarero et al., 2021; Mellert et al., 2016; Sánchez-Salguero, Navarro-Cerrillo, Swetnam, & Zavala, 2012). However, due to local adaptions (Cavin & Jump, 2017), these populations may also experience high resistance (sensu Lloret et al. 2011) to events reproducing such climatic limits, while populations growing under historical suitable conditions – i.e., located close to their core bioclimatic niche- can be more vulnerable to such drought events. On the other hand, populations living under more historical suitable climatic conditions may exhibit greater recovery, thus providing more resilience ("engineering resilience", sensu Pimm 1984) to abiotic disturbances, particularly those associated with extreme climatic events (Redmond et al., 2018). This resilience could be due to the capacity of dominant species to remain and to recover stand structural features. This can be attained by further growth of the remaining trees (Camarero et al., 2018) or/and by the recruitment of new individuals, which in turn can be favoured by the conditions arising with the die-off event (Suarez & Lloret, 2018).

Integral Projection Models (IPMs) are used to describe changes across time in a given population structured by a continuous individual variable (e.g., size) (Easterling et al., 2000). As other demographic models, IPMs provide estimates of the asymptotic growth-rate, stable size distribution, reproductive values, sensitivities and elasticities of the vital rates (Metcalf, McMahon, Salguero-Gómez, & Jongejans, 2013). IPMs are built from regression models describing vital rates -growth, survival, reproduction- from individual state variables (usually size or age) and they also can include environmental covariates (e.g., climate, competition and nutrient availability) (Merow et al., 2014). The use of IPMs in forest population’s dynamics has advantages in front of traditional population matrix models. For instance, IPMs can calculate survival, growth, and recruitment with a reduced number of data -e.g., in small populations with less than 300 individuals-. IPMs are also more pertinent when size variable is continuous (Ramula, Rees, & Buckley, 2009). Consequently, these models are broadly used in studies of the demography of forest populations and their dynamics (Dauer & Jongejans, 2013; Ferrer-Cervantes et al., 2012; Molowny-Horas et al., 2017).

Pinus sylvestris L. (Scots pine) has a wide range of distribution and is one of the most widespread tree species in the world. It is extended across many biomes with different climates, from populations placed in eastern Siberia, to relatively dry and warm locations of the Mediterranean Basin (Durrant, De Rigo, & Caudullo, 2016). Particularly, in the Iberian Peninsula *P. sylvestris* populations are located in the southern limit of its range of distribution (Matías & Jump, 2012), where the climatic conditions are less suitable for this species. Therefore, these populations can be more prone to die-off under climate change scenarios (Sánchez-Salguero et al., 2012), especially when facing recurrent and severe drought events (Vilà-Cabrera et al., 2013). During 2005 and 2006, the Iberian Peninsula experienced an important drought followed by a period of dry years (Banqué Casanovas et al. 2013; Füssel et al. 2017, see supplementary material, Figure S1) that ended up in an acute drought event in 2012 (Camarero et al., 2018). As a consequence, forest die-off appeared across many woodland areas of the Iberian Peninsula including Catalonia (Banqué Casanovas et al., 2013; Carnicer et al., 2011). Especially, *P. sylvestris* populations experienced growth reduction (Camarero et al., 2018), loss of green canopy (L. Galiano et al., 2010) and bark beetle infestations (Jaime et al., 2019) that eventually promoted tree mortality, particularly in stands with high density (Galiano et al., 2010).

Here, we built an IPM to explore the dynamics of forests dominated by *P. sylvestris* following a drought-induced mortality event. Our main goal was to project at mid-term the stand structure under different climatic scenarios. For such purpose, we specifically consider the role of the recruitment stages and include site historical climatic suitability of each site as a covariate.

Particularly, we assessed the following questions:

1) How forest die-off events affect key vital rates, such as recruitment, growth and mortality, that determine stand dynamics? Are these effects on key rates constant over time or, alternatively, exacerbated or depleted after the event? Do temporal trends of recruitment, growth and mortality differ between climatic scenarios?

2) Are the stands affected by die-off able to recover the same structure at mid-term, and under different climate change scenarios than those stands that did not experience die-off? In other words, are affected stands resilient, and does this resilience vary under different future climatic scenarios?

3.2. Methods

3.2.1. Study system

We performed the study in pure and mixed populations of *P. sylvestris* in Catalonia, North East of the Iberian peninsula placed in locations that recently experienced drought-induced forest die-off and tree mortality -due to two drought events in 2005 and 2012 - concurrent with bark beetle infestation (Serra-Maluquer et al. 2018, Jaime et al. 2019, supplementary material, Figure S1). We selected 20 populations representing the whole climatic gradient across the *P. sylvestris* range in Catalonia (Figure 1). This selection was established by visual observation during late 2012 and early 2013. Due to the orography, these populations experience different climate conditions, from wet and cold suitable conditions -in the Pyrenees- to dry and warm unsuitable conditions -in the Catalan Coastal Range. The elevation of the studied sites ranges from 600 to 1,600 m.a.s.l, the mean annual temperature ranges from 6.5 °C to 13 °C and the annual precipitation from 600 to 1100 mm per year (Karger et al. 2017, Figure 1).

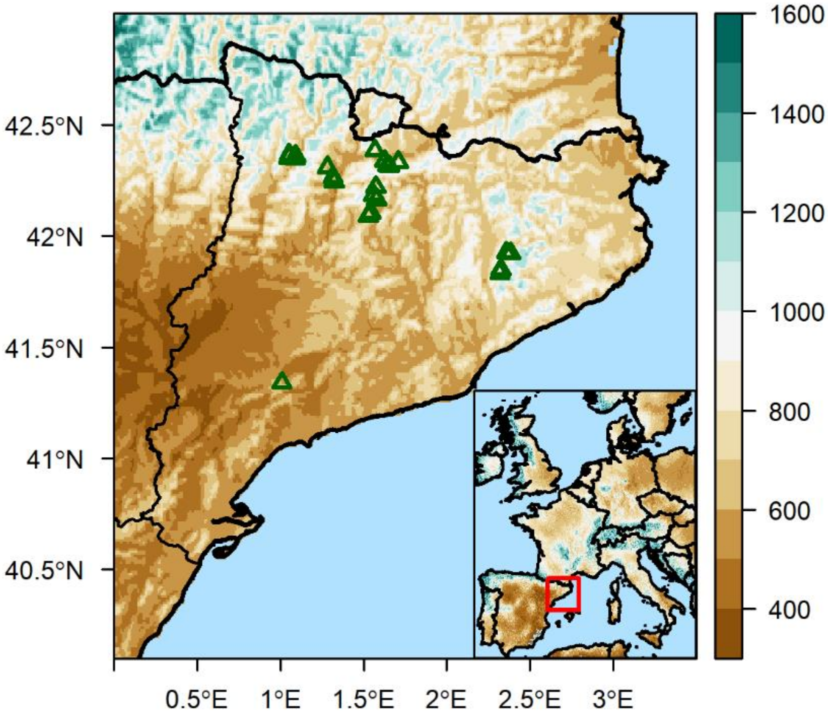

Figure 1: Mean annual precipitation (mm) in our study area. Source: Karger et al. 2017. The location of the 20 sampled *P. sylvestris* populations are represented as green triangles.

During 2013, two 10 m-diameter circular (314 m^2) plots were established in each of the 20 selected populations. In each population, we considered paired plots, one plot was set up in a stand affected by die-off and other plot in an unaffected stand (mainly located close to each other in a range of 50 to 150 meters of disatance). In affected plots, the loss of plot basal area ranged from 30% to 90%, considering the basal area of dead trees relative to the total one (supplementary material Table S1). We measured size (diameter at breast size, dbh) and distance and course from the plot centre to all alive and dead adult trees (dbh > 2.5 cm). We also recorded all the *P. sylvestris* recruits – dbh < 2.5 cm - and we classified them in two stages (i) individuals up to 1.30 m high and (ii) individuals taller than 1.30 m high. Finally, we recorded the following stand characteristics: slope, aspect, total understorey cover, tree density (trees ha^{-1}) and basal area ($m^2 \cdot ha^{-1}$). During 2017 (4 years after the first survey), we re-sampled the same plots following the same protocol to record *P. sylvestris* tree mortality, individual diametric growth, transition among recruitment stages and ingrowth to the adult stage from the recruiting ones.

3.2.2. Climatic suitability modelling

We used Species Distribution Models (SDMs) to obtain the historical climatic suitability of the studied populations. *P. sylvestris* occurrences in the Iberian peninsula (N = 10,383) were extracted from EU-Forest dataset (Mauri et al., 2017). EU-Forest occurrences dataset is based on almost 250.000 plots of National Forest Inventories of the most European countries. The use of data based on Forest Inventories allowed us to include absence data in our model. We did not consider the occurrences of the southernmost populations of the Iberian Peninsula, sited in Sierra Nevada, usually considered as a different infraspecific taxa (*P. sylvestris* var. *nevadensis*) (Olmedo-Cobo, Gómez-Zotano, & Serrano-Montes, 2017) which could show differences in niche characteristics due to local adaptations (Guisan, Thuiller, & Zimmermann, 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) and based on climatic data from 1979 - 2013 period. To calibrate the model, we used the mean of the six least correlated bioclimatic variables in all the Iberian Scots pine occurrences and absences (isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, precipitation seasonality and precipitation of wettest quarter), after testing the collinearity between nineteen explored bioclimatic variables by means the Variation Inflation Factor (VIF) (Marquaridt 1970).

The SDM algorithm used to calculate historical climatic suitability was Boosted Regression Tree (BRT), applying the “Gbm R package” 2.1.3 (Ridgeway, 2007). We built the species distribution model following the criteria used in the literature (Barbet-Massin et al., 2012; Elith et al., 2008; Pérez Navarro et al., 2018). The calibration of the model was repeated three times using k-fold cross-validation with three different training and test datasets. The final model output was based on all the occurrences. Model evaluation was based on the area under curve (AUC; Hanley and McNeil 1982) and the variance explained, as R squared coefficient (AUC = 0.9; $r^2 = 0.72$). These calculations were performed with “caret R package” (Kuhn & others, 2008).

For the calculations of the future climatic suitability, we extrapolated our model to both 2049 and 2069 years, which corresponds respectively to the average values of bioclimatic variables of 2041-2060 and 2061-2080 periods obtained from climatic scenarios based on future Representative Concentration Pathways (RCP): RCP 4.5 and RCP 8.0; used in the Intergovernmental Panel on Climate Change (IPCC) scenarios. These bioclimatic variables were provided by CHELSA climate database (Fick & Hijmans, 2017). To make the change of climatic suitability progressive and not stepper, we interpolated climate suitability for each year between 2017 and 2049 and between 2049 and 2069. We also extrapolated our SDM to the current climate reference data (1979 – 2013) to build up a stable climate scenario as a control.

3.2.3. Integral projection modelling

We used IPMs as a tool to simulate population dynamics and to project future forest structure. IPMs are applied to populations whose structure is best described by a continuous variable (in our case, dbh as a proxy for tree size), as opposed to matrix population models, which require a previous classification into discrete classes. Population dynamics in the IPM methodology is generally characterized by three vital rates, namely growth, survival and reproduction. In this study, we have assumed that those vital rates depend on dbh as well as on a set of environmental covariates (i.e., competition and climatic suitability) through different analytical expressions (see below). The input and output of a single run of an IPM consist of the continuous distribution of the number of individuals (trees, in this study) at times t and $t + \Delta$, where $\Delta = 4$

years in the present work. Vital rates operate on the continuous input distribution of the number of trees per dbh, *n(dbh, t)* through an integral equation, to yield the continuous output distribution $n(dbh,\ t + \Delta)$. Due to its complexity, the integrals in the IPM methodology are usually solved by means of numerical quadratures. The resulting distribution $n(dbh,\ t + \Delta)$ can then be used to calculate structural variables such as tree density, basal area and mean diameter. We describe below the different vital rates regression used to build the final IPM.

Survival

Survival is described as the probability of a given adult tree to survive at time $t + \Delta$ as a function of tree size and other environmental and plot-related variables (Coulson, 2012). We could not calculate this probability directly from our plots since we did not find enough mortality cases between the two censuses (2013 and 2017). Thus, we used Spanish National Forest Inventory (IFN) data (DGCN, 2007) to build our survival function. We assumed that the studied plots are representative of *P. sylvestris* forests in the region, thus, the determinants of mortality extracted from this database overall correspond to those operating in these plots. We applied a general linear model with a binomial error structure to explain survival tree probability. Plot basal area, and both individual size at time 0 (dbh_{t0}) and at time t1 (dbh_{t1}), were used as mortality predictors (Table 1). Previous exploratory studies of *P. sylvestris* mortality using IFN data showed that baseline mortality (in the absence of extreme drought events or other disturbances) is mainly related to the stand competition and not to climate conditions across Spain (Ruiz-Benito, Lines, Gómez-Aparicio, Zavala, & Coomes, 2013). Accordingly, the inclusion of plot basal area in the survival function aimed to consider in the model these competition effects. Furthermore, we assumed that our simulations can be conservative since lagged mortality affectation due to acute drought (Bigler et al., 2007; Klockow, Vogel, Edgar, & Moore, 2018) was not captured, i.e., the same survival rate after the drought event was applied to paired affected and unaffected plots. In addition, mortality following the event could have been underestimated since we only have data for 4 years after 2013, and later drought-induced mortality may have occurred after such a short time interval.

Growth

Tree growth is defined as the increment of size (dbh_{t1} – dbh_{t0}) during a given time interval (in our case, 4 years). We calculated a growth function using Generalized Additive Models for location, scale and shape (GAMLSS) using “gamlss R package” (Stasinopoulos & Rigby, 2007). We estimated mu coefficient (scale, mean) as a function of basal area (BA), tree plot density (N), climatic suitability (CS), individual size (dbh_{t0}) and die-off affectation (yes or not). Sigma coefficient (scale) was estimated from basal area and dbh at t_0 (Table 1).

Recruitment/Ingrowth

Ingrowth is defined as the increment of the number of new adult trees during a given time interval (in our case, 4 years), i.e., the number of saplings that become adults. Since in perennial plants, seedlings and saplings often have different requirements and vital rates than adult trees (Bertrand, Gégout, & Bontemps, 2011), we discretised different recruit classes: seedlings, saplings and ingrowth trees (small adults, ingrowth hereafter). Because we had data of the total amount of seedlings, saplings and ingrowth trees in each plot, we could compute a regression for the total number of individuals in each of these three recruitment discrete stages using environmental covariates (basal area and climatic suitability), previous number of recruits of each discrete stage (expressed as n1 for the number of seedlings, and n2 for the number of saplings) and die-off affectation -as a factor- (Table 2). We assume that the number of seedlings (n1) does not depend on the size of the adult trees in the plot. Since plots without recruitment stages were common, we built the recruitment functions as zero-inflated regressions. We used “pscl R package” (Jackman et al., 2020) to calculate these models.

Table 1: General linear model with binominal distribution and GAMLSS terms for survival and growth, respectively, at the plot level. Dependent variables were: basal area (BA, m^2 ha^{-1}), dbh at t_0 and t_1 (cm.), tree density (N, number of trees · ha^{-1}), climatic suitability (CS) and die-off affectation (yes/no).

Function	*Family Model*		*Intercept*	*BA*	*$dbht_0$*	*$dbht_1$*	*N*	*CS*	*Die-off [Yes]*
Survival	**Binomial**		3.335	-0.961	0.080	-0.001	-	-	-
Growth	**GAMLSS**	***Mu coeff.***	-2.122	-0.506	0.022	$-2.00 \cdot 10^{-4}$	-0.007	2.901	-
		Sigma coeff.	-0.274	0.157	-0.004	-	-	-	-0.120

Table 2: Zero-inflated regression models terms (columns) for total number of seedlings, saplings and ingrowth at time (t_1). Variables represented in rows are $n1_{t0}$: Number of seedlings at t_0 (number of seedlings · ha^{-1}), $n2_{t0}$: number of saplings at time t_0 (number of saplings · ha^{-1}). Other environmental variables used were basal area (m^2 ha^{-1}), climatic suitability, and die-off affectation (yes/no).

	n. seedlings t_1	***n. saplings t_1***	***n. Ingrowth t_1***
Count component			
Intercept	-5.4804	1.3143	-3.7629
Basal Area	-2.727	-0.3831	-9.6048
(Basal Area)$^{0.5}$	4.7794	-	12.0489
$n1_{t0}$	0.0173	0.0105	-
$n2_{t0}$	-	0.0537	0.1234
Climatic Suitability	7.1219	-	-
Die-off [Yes]	-1.0247	-	-
Zero component			
Intercept	-0.6138	2.5618	3.895
$n2_{t0}^{0.5}$	-	-2.8698	-3.295

Simulation

Our IPM was built by combining calculated vital rates using numerical integration with the Alternative Extended Simpson (Press, Flannery, Teukolsky, & Vetterling, 1989) numerical quadrature rule (we used a value of 0.147 cm). IPM outputs were individual sizes in terms of dbh. The upper and lower limit of adult individual size were established as 150 cm and 2.5 cm of dbh, respectively. We can extract several plots characteristics from the IPM outputs (individual tree size) such as tree plot density, basal area, plot mean diameter, plot seedling and sapling density and ingrowth density (as density of saplings that became adult in each model step, i.e., in 4 years). Climatic suitability was used as environmental covariable to capture how future climate trends affect *P. sylvestris* forest dynamics. Thus, we simulated the IPM using climatic suitability under three different climate scenarios: current constant climate (1979-2013 reference period), and climate change scenarios corresponding to RCP4.5, and RCP 8.0 projections; for both types of plots -affected by die-off and unaffected - during 52 years (2017 – 2069) in 4 year's steps. We simulated forest dynamics under a hypothetical absence of new die-off events.

3.2.4. Statistical analyses

First, we built different Generalized Mixed Models (GLMMs) to assess how die-off event determined stand dynamics over time after the event, considering different future climatic scenarios. Each plot was used as a replicate. Models' response variables were, respectively: (1) basal area, (2) seedling density and (3) ingrowth density (density of trees that became adult at given model time step), all of them extracted from IPM projections. The models' explanatory variables were: die-off affectation (yes-not), climatic scenario (constant climate, RCP4.5, RCP8.5) and time (years) after the die-off event. Die-off affectation was also included as random effect. In the model was also included the interaction between die-off affectation and time, and the interaction between die-off affectation and climatic scenario.

Second, we also built a GLMM to assess the resilience capacity at mid-term (projections to 2069 year). For such purpose, here we used several IPM outputs for the 2069 year as response variables: (1) basal area, (2) tree density (N), (3) seedling density, (4) saplings density, (5) ingrowth and (6) mean diameter. We used climatic scenario and die-off affectation and their interaction as explanatory variables. In this way, we tested if at mid-term period of time, the structure of die-off affected plots will differ from unaffected ones and if the climatic scenario will reduce resilience. Therefore, significant diminution of response variables in plots affected by die-off would mean a loss of resilience.

3.3. Results

3.3.1. Integral Projection Modelling

We found that survival probability was negatively related to plot basal area and tree diameter at time t_1, while it was positively related to the dbh at t_0 (Table 1). This suggests that bigger trees, with likely lower growth rate are less prone to die. The negative effect of basal area denotes that competence had a negative effect on tree survival. Also, tree growth was negatively related to those variables associated with competence (basal area and tree density) and dbh. Conversely, tree growth was positively related to climatic suitability (Table 1). Regarding recruitment stages, seedlings, saplings and ingrowth densities were negatively related to basal area. On the contrary, both seedling and sapling densities were positively associated with seedlings density at t_0. Additionally, saplings and ingrowth densities were positively related to the number of saplings at time t_0, while seedlings density were positively influenced by climatic suitability as well (Table 2).

3.3.2. Forest structure and recruitment across time

During the 2017 – 2069 projected period we found significant correspondences between the structural and demographic variables -basal area, seedlings density, saplings density, ingrowth density, tree density, mean tree diameter- and die-off affectation, climate scenario, or time since the die-off event. In particular, basal area, saplings density and mean diameter were positively related to time since the die-off event. On the other hand, both seedling density, ingrowth density and tree density were negatively related to year since die-off event. (Table 3, Figure 2). Across time, die-off affected plots significantly showed smaller basal area, and less adult tree densities. Conversely, they showed greater ingrowth, seedling and sapling densities. These effects remained throughout the whole simulated period (Figure 2). Projections under climate change scenarios (RCP4.5, RCP8.0) led to a reduction of basal area, adult and seedling densities, as well as to an increase of ingrowth density, compared to the projections using constant current climate.

Table 3: Results of the first GLMM, built to asses the determinants of stands dynamics across time, for the response variables: basal area, seedling density, ingrowth density, sapling density, mean diameter and tree density for the whole period; considering time since the die-off event -year (time)-, die-off affectation [yes *vs* no] and climate change scenarios, -abbreviated as CCscenario- [RCP4.5, RCP8.0 vs. current constant climate] as explanatory factors. The estimates and significance (*p* value) of the factors for the response variables are represented in rows. Interactions between factors are also included. The variance explained by the fixed effects of the models -r^2m- are represented in the last row.

	Basal area		**Seedling density**		**Ingrowth density**	
	Estimate	*p*	Estimate	*p*	Estimate	*p*
Intercept	-0.083	<0.0001	3.749	<0.0001	-0.522	<0.0001
Die-off [Yes]	-0.598	0.0020	1.168	<0.0001	1.698	<0.0001
CCscenario[RCP4.5]	-2.819	<0.0001	-0.429	<0.0001	0.422	<0.0001
CCscenario[RCP8.0]	-2.670	<0.0001	-0.393	<0.0001	0.398	<0.0001
Die-off [Yes]:RCP45	0.207	0.5940	-0.307	<0.0001	-0.198	0.104
Die-off [Yes]:RCP80	0.219	0.5738	-0.285	<0.0001	-0.189	0.122
Year (time)	0.430	<0.0001	-0.071	<0.0001	-0.047	<0.0001
Die-off [Yes]:Year	0.019	0.0426	0.021	<0.0001	0.121	<0.0001
r^2m	*0.51*		*0.49*		*0.329*	

Table 3. Extended:

	Saplings density		***Mean Diameter***		***Tree Density***	
	Estimate	*p*	*Estimate*	*p*	*Estimate*	*p*
Intercept	-2.834	<0.0001	2.860	<0.0001	6.759	<0.0001
Die-off [Yes]	0.054	<0.0001	-8.631	0.179	-8.805	<0.0001
CCescenario[RCP4.5]	0.034	0.466	-2.964	0.0002	0.004	0.770
CCescenario[RCP8.0]	0.032	0.494	-2.889	0.0003	0.005	0.750
Die-off [Yes]:RCP45	-0.075	0.258	-0.191	0.109	-0.198	0.104
Die-off [Yes]:RCP80	-0.071	0.283	-0.160	0.151	-0.189	0.122
Year (time)	0.101	<0.0001	0.571	<0.0001	-0.015	<0.0001
Die-off [Yes]:Year	0.008	0.260	0.023	<0.0001	0.057	<0.0001
r^2m	*0.41*		*0.16*		*0.14*	

Also, significant interactions emerged in our GLMMs comparing climatic scenarios. There were positive interactions between the effect of die-off affectation and time since the die-off event for basal area, seedling density, ingrowth density, mean diameter and tree density (Table 3). A negative interaction between climate change scenario and die-off affectation emerged in the model with seedling density as response variable. In the other structural variables, there was not interaction between die-off and climate change scenario. This indicated that temporal patterns of future simulated basal area, ingrowth density, mean diameter and tree density differed according to die-off affectation of the plot -showing a higher increase of these response variables in die-off affected plots- independently of climate change scenario~~.~~ Overall, we observed at a mid-term a convergent pattern of plot basal area among the die-off affected and the unaffected plots, since plots that experienced die-off showed a higher increase of basal area than unaffected plots (Figure 2) over time. Regarding the temporal dynamics of seedlings and ingrowth density, the decrease across time was higher in die-off affected plots than in unaffected ones, thus emerging also a convergent pattern of the density of both seedling and ingrowth stages between die-off affected and unaffected plots (Figure 2). The negative interaction between die-off affectation and climate change scenario on seedlings density, showed that the positive effect of the die-off affectation on seedlings density is negatively modulated by warmer climate change scenario. Climatic change scenarios (both RCP4.5 and RCP8.0) induced a diminution in seedlings density, resulting in fewer differences between affected and unaffected plots when comparing climate change projections with constant climate projections (Figure 2).

3.3.3. Projected forest structure at mid-term

At the end of our projections (2069 year, i.e., 56 years since the die-off event), basal area and tree mean diameter were still significantly lower in plots that were affected by die-off than in unaffected ones (Figure 2, Table 4). Moreover, these affected plots had a higher number of seedlings, saplings and ingrowth densities, resulting overall in a higher density of young trees.

However, the 2013 die-off event did not cause significant changes in adult tree density (Table 4).

The GLMM also showed that, in addition to die-off, climate change scenario influenced almost all the above-mentioned structural variables: basal area, seedlings density, saplings density, ingrowth density and mean diameter (Table 4). Projections using warmer RCP4.5 and RCP8.0 climate scenarios resulted in significantly lower basal area than projections using a constant current climate (1979-2013) scenario. Seedling density was also lower in both warmer climate change scenarios than in projections using a constant reference climate. However, projections using warmer climate change scenarios showed higher densities of saplings and ingrowth rate than projections using constant climate. Overall plot tree density did not significantly differ between the affected and unaffected plots, neither between climate scenarios. Significant negative interaction between die-off affectation and climate scenario emerged for basal area, seedlings density, saplings density and mean diameter models. This interaction is translated to a higher basal area difference between affected and unaffected plots in both climate change scenarios (RCP 4.5 and RCP 8.0 with harsher climatic conditions than current climate) at 2069 in comparison to projections using constant current climate. Contrarily, this interaction shows how the positive effect of the die-off on densities of these stages -seedlings and saplings- was attenuated when considering these warmer climate scenarios. Besides, the recovery of the mean diameter in plots affected by die-off was significantly lower for climate change scenarios than for constant climate scenarios.

Table 4: Results of the second GLMM, for the response variables at the final of the projected period (year 2069) basal area, seedling density, ingrowth density, sapling density, mean diameter and tree density, considering die-off affectation [yes *vs* no] and climate change scenarios, -abbreviated as CCscenario- [RCP4.5, RCP8.0 vs. current constant climate CCscenario] as explanatory factors. The estimates and significance (*p* value) of the factors for the response variables are represented in rows. Interactions between factors are also included. The variance explained by the fixed effects of the models -r^2m- are represented in the last row.

	Basal area		***Seedling density***		***Sapling density***	
	Estimate	*p*	*Estimate*	*p*	*Estimate*	*p*
Intercept	4.095	<0.0001	2.660	<0.0001	47.628	<0.0001
Die-off[yes]	-0.477	0.0002	1.249	<0.0001	43.224	<0.0001
CCescenario[RCP4.5]	-0.123	<0.0001	-0.619	<0.0001	5.675	<0.0001
CCescenario [RCP8.0]	-0.112	<0.0001	-0.487	<0.0001	5.438	<0.0001
Die-off[Yes]:RCP4.5	-0.081	0.024	-0.391	0.0116	-7.935	<0.0001
Die-off[Yes]:RCP8.0	-0.076	0.034	-0.361	0.0194	-7.317	<0.0001
r^2m	*0.30*		*0.53*		*0.47*	

Table 4. Extended:

	Ingrowth density		***Mean diameter***		***Tree density***	
	Estimate	*p*	*Estimate*	*p*	*Estimate*	*p*
Intercept	-2.331	<0.0001	3.458	<0.0001	6.521	<0.0001
Die-off[yes]	3.297	<0.0001	-0.285	0.0084	-0.091	0.0084
CCescenario[RCP4.5]	1.178	<0.0001	-0.075	<0.0001	5.675	<0.0001
CCescenario[RCP8.0]	1.095	<0.0001	-0.069	<0.0001	5.438	<0.0001
Die-off[Yes]:RCP4.5	-0.391	0.0538	-0.057	0.0150	-7.935	<0.0001
Die-off[Yes]:RCP8.0	-0.362	0.0734	-0.052	0.0251	-7.317	<0.0001
r^2m	0.40		0.19		0.10	

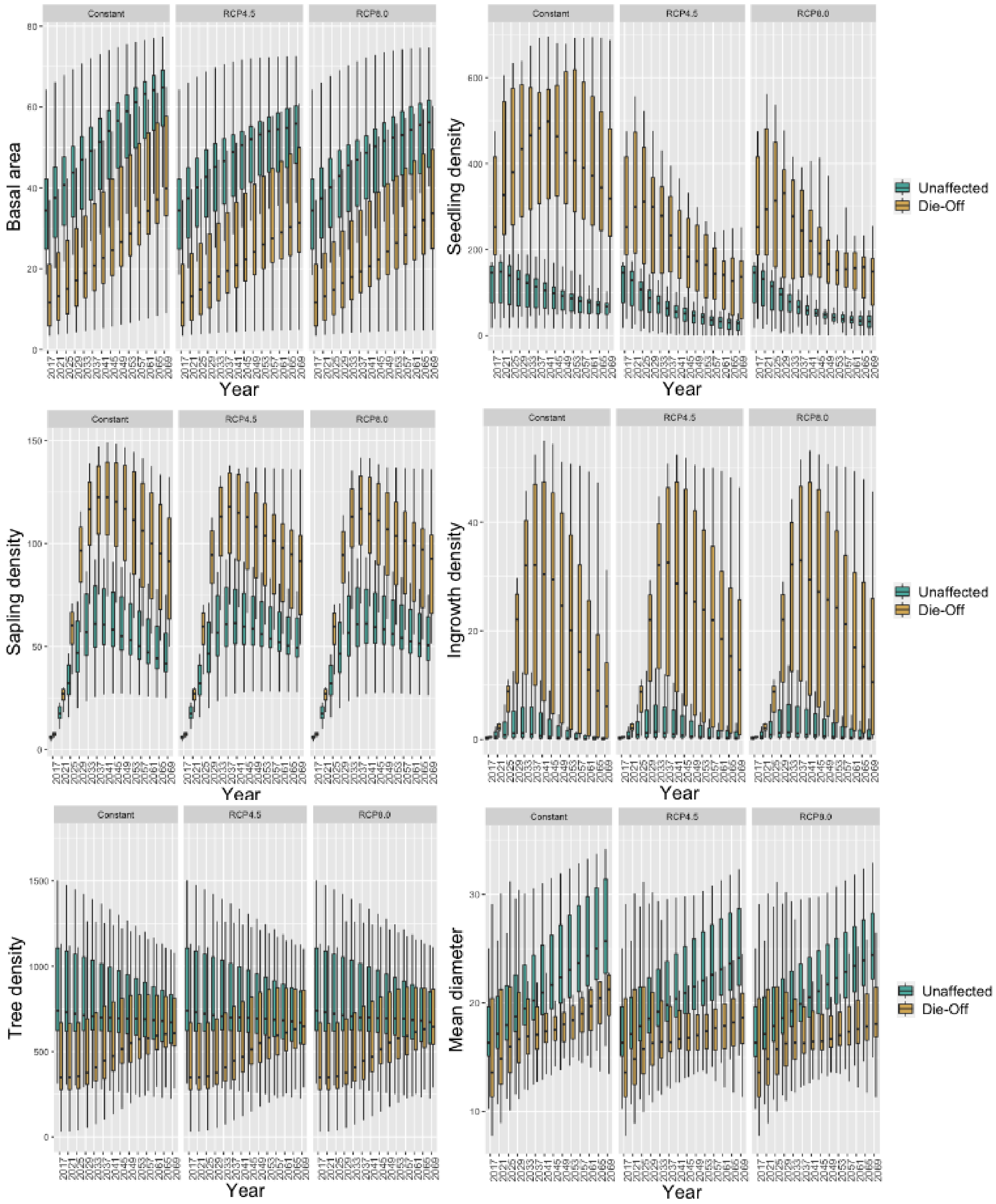

Figure 2: Structural and demographic variables of the plots extracted from IPM outputs: basal area, seedling density, sapling density, ingrowth density, tree density (adult tree density), mean diameter, for plots with die-off and for unaffected ones, under different climatic scenario (Constant -current climate- *vs*. RCP4.5 and RCP8.0). Represented as boxplots. Boxes indicate the interquartile range of the response variables obtained in the simulations, black lines indicate standard deviation above and below the mean.

3.4. Discussion

Drought-induced die-off events produce changes in both forests structure and demography dynamics that persist at mid-term, as supported by our *P. sylvestris* study case. After 52 years of simulations, plots that formerly exhibited heavy die-off still have distinct structure characteristics: less basal area, smaller mean tree size and higher density of young trees (seedlings, saplings and ingrowths). Climate change scenarios exacerbate or mitigate these trends. The overall result is that the resilience of these forests in terms of basal area is not fully attained, in our case at a temporal scale of around half-century, since this structural characteristic of forest remains with lower values in plots affected by heavy die-off than in unaffected ones.

3.4.1. Post die-off regeneration dynamics

Regarding the temporal dynamics of recruitment, the 2013 die-off event will induce a positive effect on seedlings density at both short and mid-term scenarios (up to year 2069). However, seedling density and ingrowth overall diminish across time, as expected in forest succession, while the canopy gets closed (Oliver, Larson, & others, 1996). This decrease across time was lower in die-off plots, consistent with a positive effect on the recruitment of die-off, due to gap opening. This effect would remain at mid-term (up to 2069), likely because canopy closure will persist lower in die-off affected plots, as supported by their smaller basal area, than in unaffected plots. At short-term, canopy openness in these perturbed plots is expected to promote an increase of both establishment and survival of the seedlings (Macek et al., 2017), especially in species such as *P. sylvestris*, which has a semi-intolerant shade character (Castro, Zamora, Hódar, & Gómez, 2004; Niinemets & Valladares, 2006). On the other hand, the reduction of the climatic suitability for this species during the following years after the event due to climate change will be translated into a decline in the number of seedlings, particularly in plots that experienced die-off (see interaction between die-off state and climate scenario,

Table 3). In this way, the positive effect on seedlings abundance due to canopy openness created by tree mortality resulting from die-off would be attenuated by the decline of climatic suitability during the following years (up to 2069). Other studies also highlight the *P. sylvestris* seedlings capacity to establish and compete in forest gaps, although this capacity is jeopardised in populations near to the species' climatic tolerance limit (Galiano, Martínez-Vilalta, Eugenio, Granzow-de la Cerda, & Lloret, 2013; Vilà-Cabrera et al., 2013).

3.4.2. Mid-term plot structure projections and resilience

In turn, basal area and tree density in affected and unaffected die-off plots will hypothetically converge with time in our simulations, indicating that (i) in die-off affected plots, growth rates of surviving trees would be higher than in unaffected plots, (ii) adult mortality would be lower in affected plots than in unaffected plots, and (iii) seedling establishment and higher densities of younger trees, resulting in more net ingrowth, would be higher in affected plots. Overall, this higher basal area increment in die-off plots is likely enhanced by a reduction of competence for light, nutrients and water (Nambiar & Sands, 1993). This is consistent with other studies finding that less dense tree populations should be more resistant in front of future droughts and heat-waves (Bottero et al., 2017). Also, more growth resistance has been observed in managed or thinned stands during climatic change-driven perturbations (Aldea et al., 2017). Our results suggest that self-thinning induced by drought events could also lead to an increase of post-drought growth and hypothetically to more resistant stands to further disturbances. These compensatory resilience mechanisms seem to operate even at mid-term, as seen by the convergence trend of basal area in affected and unaffected plots with time, promoted by the establishment of new individuals (seedlings) during the following years of the die-off event and the consequent high ingrowth.

However, according to our projections, the differences in basal area between the two types of plots would remain significant in 2069, in spite that basal area in affected plots would reach in

2069 similar values than those observed in unaffected plots in 2013. This is due to the long time needed to replace large trees which died during the drought event. This is reflected in the lower tree density during the next years after the drought, and in the smaller tree size (in average) throughout the whole period in affected plots. Overall, in the absence of further disturbances, full resilience would occur beyond 2069 in our simulations, when plots with previous die-off would eventually reach similar levels of basal area than unaffected plots. We also observed that adult tree density in die-off plots will reach the same values as unaffected plots by 2069, approximately. Nevertheless, this is not translated in a similar value of total plot basal area, as said above. In plots with die-off affectation, ingrowth is higher, likely due to the release of competence and the increase of both seedlings and saplings establishment and survival; as a consequence, adult trees of die-off plots could be generally younger and thinner than the individuals of not affected plots. This pattern of forest regeneration, with younger individuals and high turnover rates, is consistently observed abroad when the regime of forest disturbances is modified by extreme climatic events such as droughts (McDowell et al., 2020).

3.4.3. Future perspectives

Nevertheless, our simulations did not consider future drought events and we assumed that mortality was driven by competence instead of climatic suitability. This assumption is supported by the fact that we did not find any significant correlation between the historical climate variables and mortality rates in the Spanish *P. sylvestris* plots sampled in the IFN, differently to other studies (Zhang, Huang, & He, 2015). But, mortality and die-off will be conditioned by the emergence of the extreme climatic events such as droughts and heat-waves (Lloret & Kitzberger, 2018), pushing back succession or even provoking the collapse of these forest communities (Harris et al., 2018).

At mid-term, scenarios of warmer climate would result in a diminution of basal area in plots affected by die-off, likely due to reduced growth in *P. sylvestris* trees (Table 1). Growth patterns of *P. sylvestris*, including growth recovery and resilience after drought, are highly related to climatic conditions, especially to temperature and potential evapotranspiration (PET) prior and past the drought event (Hereş et al., 2012). Thus, future warmer climates are expected to induce growth decline and loss of resilience across Catalonian region (Bose et al., 2020), as we also observed in our results. The mechanisms involved in this predicted reduction of resilience include the partial or total hydraulic failure of trees (Adams, Zeppel, Anderegg, Hartmann, Landhäusser, Tissue, Huxman, McDowell, et al., 2017), and the loss of leaf area and depletion of carbon reserves (Galiano et al., 2011), which eventually can lead to delayed mortality (Jump et al., 2017).

Self-thinning induced by die-off could bring populations to a new situation with less basal area and therefore with less intraspecific competition, that, in turn, will be hypothetically more resistant to future climatic events (Sohn, Hartig, Kohler, Huss, & Bauhus, 2016). But, populations close to their climatic tolerance limit could be even less resilient at mid-term, since the establishment of *P. sylvestris* seedlings could be less than the recruitment of other coexisting species (Galiano et al., 2013; Vilà-Cabrera et al., 2013). Concurrently, a continuous reduction of climatic suitability will diminish this seedling establishment at mid-term, as seen in our results. Besides, future droughts and xeric conditions may cause seedling establishment decline after disturbances such as wildfires (Elvira et al., 2021) and windthrows (Csilléry et al., 2017) thus increasing the risk of loss of resilience of these populations. On the other hand, ingrowth will increase under future warm climate conditions (as expected in RCP4.5 and RCP 8.0 scenarios), due to (1) niche differentiation of this age class, which may also experience facilitation (Canham & Murphy, 2017), (2) better ability of younger trees to survive and grow in warmer conditions (Peltola et al. 2002, Margalef et al. in prep) and (3) release of intraspecific competition with gap opening (De Chantal, Leinonen, Kuuluvainen, & Cescatti, 2003). However, this increase of new adults will not be translated into a higher plot basal area, at the time scale considered, instead it would lead to younger forests with thinner trees (McDowell et al., 2020).

3.4.4. Assessing population dynamics and resilience using IPMs

Under climate change, dendroecological studies suggest a growth decline at tree-level in the rear-edge distribution of *P. sylvestris* population, due to an increase in water deficit (Camarero et al., 2021; Hereş et al., 2012). This tendency can eventually lead to the tree death. Nevertheless, few studies have addressed growth and resilience at plot level after drought-induced die-off events, considering the response of the remaining trees. The use of demographic models such IPMs is an appropriate tool to assess future tendencies of tree populations in forests (Molowny-Horas et al., 2017; Sánchez-Velásquez, Pineda-López, Ibarra-Zavaleta, & López-Serrano, 2021). A key point of our research is the coupling of seedlings and saplings dynamics with growth and survival functions, as well as the introduction of climatic suitability as a covariate. This integration allows capturing a continuous picture of changes in plot structure across the projection time-lapse. Besides, the use of IPMs, allows us to analyze how self-replacement is determined by climate change and die-off events (Batllori et al., 2020), in contrast to dendroecological approaches that do not consider regeneration dynamics, thus, underestimating resilience at population level. This study highlights the relevance of integrating the dynamics of the different age classes (Ettinger & HilleRisLambers, 2013), particularly of recruiting stages, at plot level, in which interacting mechanisms such as climate and competence could distinctly operate in sites with different degrees of drought-induced affectation.

3.5. Conclusions

Forest mortality concern is increasing as a consequence of the intensification of the drivers that provoke die-off events, as we expect in the near future climate change scenario. Some studies have suggested loss of forest growth and resilience after drought events (Bose et al., 2020) and the likelihood of vegetation shifts (Batllori et al., 2020). But not enough time has passed since most of such events were recorded to know the consequences at mid and long term. Although simulations do not predict the future, they allow analyzing how current die-off events can influence future population dynamics. For such purpose, IPMs constitute a useful tool, since they allow to assess the relevance of the different processes that determine forests dynamics and structure.

Our results show that despite the capacity of Catalonian *P. sylvestris* forests to recover their structure after drought-induced die-off events, largely due to the recruitment and growth of young trees, this recovery does not appear to be immediate. Yet the effects of these events could remain for long periods, mostly due to the loss of large trees during the drought events, which can only be replaced by new trees after several decades. This reduced resilience would diminish even more under climate change scenarios that imply extreme episodes of high temperature and water stress.

Acknowledgements

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Supplementary material

Chapter 3

Table S1: Characterization of the 20 populations used in this study. The plot ID was composed by both one number and one letter. The number identify the population while letter means the forest die-off affectation – A: affected, B: unaffected- Here we also showed accompanying forest canopy species, dominant understory composition, total plot basal area (BA, m^2 ha$^-$), tree density (N, number of trees · ha-1) and relative dead basal area (dead BA, %).

ID	**Longitude**	**Latitude**	**Accompanying canopy species**	**Understory species**	**BA**	**N**	**Dead BA (%)**
1A	1,5770	42,1644	-	*Juniperus communis*	25,8	2070,1	46,4
1B	1,5771	42,1641	-	*Buxus sempervirens, J. communis*	32,4	1560,5	1,1
2A	1,5433	42,1046	-	*J. comunis, Rosa sp.*	4,8	254,8	74,6
2B	1,5440	42,1050	*Quercus pubescens, Quercus ilex., Sorbus sp.*	*B. sempervirens*	21,8	796,2	4,6
3A	1,5736	42,2202	*Pinus nigra*	*B. sempervirens, J. communis*	16,7	1401,3	55,7
3B	1,5733	42,2212	*P. nigra*	*B. sempervirens, Rosa sp.*	30,7	2356,7	2,9
4A	1,6424	42,3175	*Q. pubescens*	*B. sempervirens, J. communis*	6,3	414,0	68,6
4B	1,6427	42,3173	-	“”	32,3	1082,8	5,3
5A	1,6532	42,3137	-	“”	4,2	318,5	90,6
5B	1,6531	42,3133	-	“”	62,3	828,0	14,4
6A	1,6252	42,3370	-	*Amelancher ovalis, J. communis, Rosa sp.*	26,6	318,5	46,9
6B	1,6247	42,3369	*P. uncinata*	*Prunus spinosa, Rosa sp.*	40,7	1337,6	2,0
7A	1,5672	42,3839	*P.uncinata*	*B. sempervirens, J.communis*	33,7	541,4	29,1
7B	1,5676	42,3838	-	*J. communis*	39,0	732,5	20,3
8A	1,7094	42,3324	*P. uncinata, Prunus avium*	*A. ovalis, Rosa sp.*	34,6	414,0	58,1
8B	1,7096	42,3321	-	*J. communis*	65,0	509,6	6,0
9A	1,3231	42,2437	-	*Arctostaphilos uva-ursi, J. communis*	3,5	668,8	88,3
9B	1,3217	42,2431	*J. communis*	“”	29,6	1082,8	3,0
10A	1,3162	42,2649	-	*J. communis*	5,9	350,3	73,7
10B	1,3168	42,2645	*P. nigra*	“”	22,2	541,4	12,6
11A	1,2812	42,3084	*P. avium*	*B. sempervirens, Rosa sp*	8,9	764,3	70,5
11B	1,2792	42,3084	-	“”	40,7	1337,6	11,0
12A	1,5296	42,0911	*Q. ilex, Q. pubescens.*	*B. sempervirens , J. communis*	11,8	955,4	68,6
12B	1,5303	42,0913	*Acer opalus*	“”	40,5	3312,1	1,7
13A	1,5596	42,1843	*P. uncinata*	“”	14,7	1114,6	50,0
13B	1,5597	42,1839	-	*C. vulgaris, Erica arborea, J. communis*	23,6	1051,0	6,1
14A	2,3841	41,9218	*Q. ilex*	*Arbutus unedo, C. vulgaris, E. arborea*	11,2	541,4	62,2
15B	2,3249	41,8483	*Q. ilex*	*C. vulgaris, E. arborea, J. communis*	19,5	891,7	22,2
16A	2,3182	41,8338	*Q. pubescens*	*C. vulgaris, Cistus laurifolius.*	15,0	605,1	45,0
16B	2,3173	41,8340	*Q. pubescens*	“”	21,6	796,2	0,0
17A	2,3584	41,9260	*Q. ilex, Q. pubescens*	*A. unedo, E. arborea., Rosa sp.*	18,7	1751,6	46,3
17B	2,3581	41,9263	*Q. ilex, Q. pubescens.*	*A. unedo, E. arborea*	26,3	1783,4	11,6
18A	1,0887	42,3479	*P. nigra*	*A. ovalis, Lonicera sp, Rosa sp.*	19,6	1178,3	25,1
18B	1,0882	42,3478	*P. nigra*	*B. sempervirens*	27,6	700,6	8,8
19A	1,0912	42,3590	*Q. pubescens, A. monspessulanus*	“”	15,1	668,8	54,8
19B	1,0897	42,3585	-	“”	28,8	605,1	4,3
20A	1,0506	42,3529	*P. nigra*	“”	17,8	573,2	50,7
20B	1,0499	42,3532	-	“”	33,7	764,3	8,3
22A	1,0086	41,3388	*Q. ilex.Q. pubescens*	*A. unedo, E. arborea*	15,7	2133,8	62,9
22B	1,0088	41,3386	*Q. ilex Q. pubescens*	*A. unedo*	56,8	2070,1	5,7

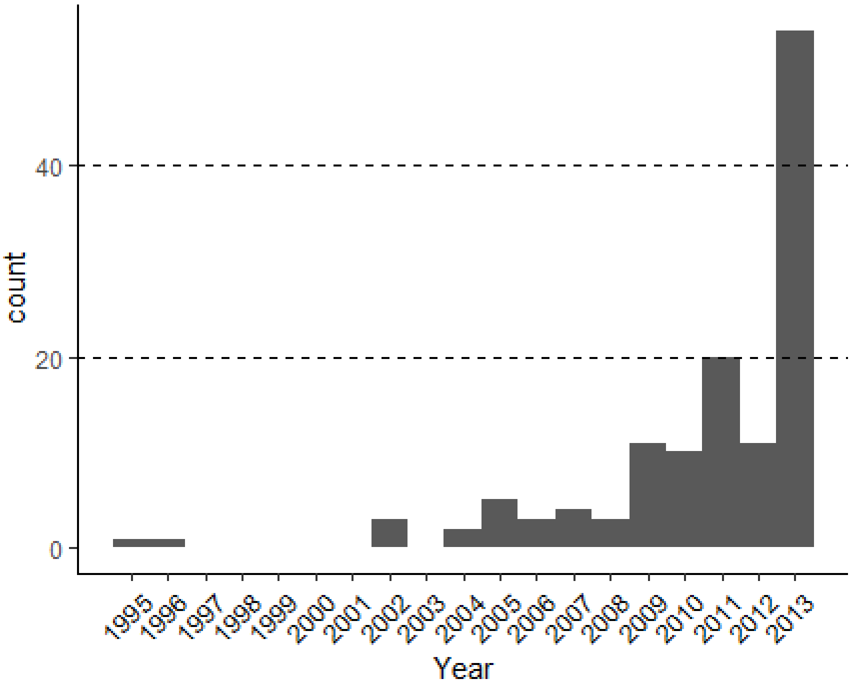

Figure S1: Year of death of a representative sample of the decayed tree.

Chapter 4

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

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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.

4.1. 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?

4.2. Material and methods

4.2.1. 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.

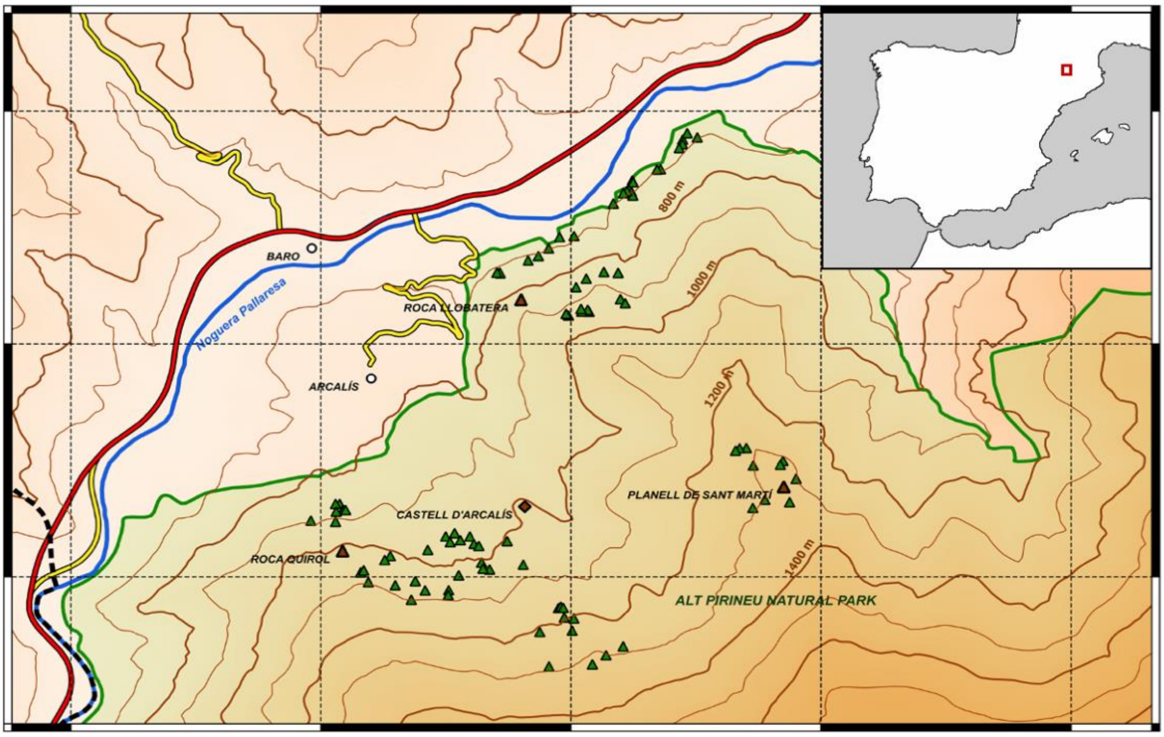

Figure 1: Location of the 88 studied individual trees (green triangles) along the altitudinal gradient in Arcalís Forest (Soriguera municipality, Spain).

4.2.2. 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.

4.2.3. 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).

4.2.4. 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.

4.2.5. 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).

4.3. Results

4.3.1. 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).

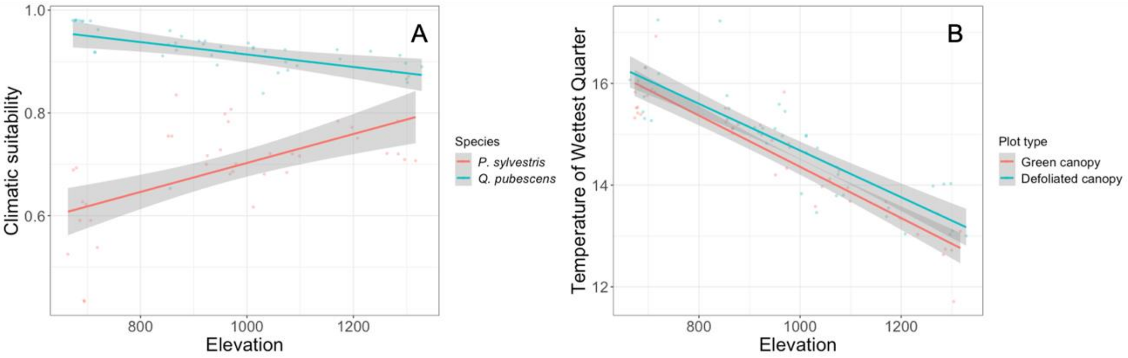

Figure 2. A: Relationship between species climatic suitability and elevation for *P. sylvestris* and *Q. pubescens* (differentiated by colour). B: Relationship between mean temperature of the wettest quarter (ºC) and elevation for green and defoliated canopies, showing higher temperature under defoliated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

4.3.2. 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).

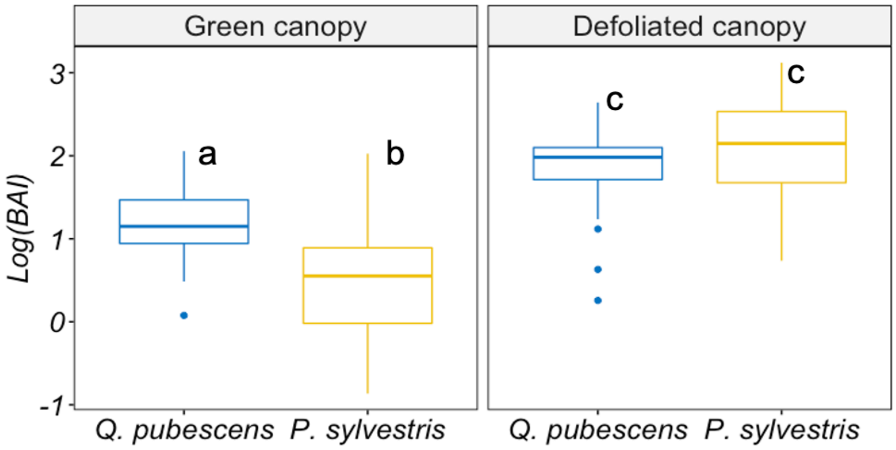

Figure 3: Boxplot panels indicating tree growth (log-transformed BAI) of understorey *Q. pubescens* and *P. sylvestris* individuals under green canopy (left panel) and defoliated canopy (right panel). Blue boxes represent *Q. pubescens* BAI and yellow boxes represent *P. sylvestris* BAI. The different 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

4.3.3. 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

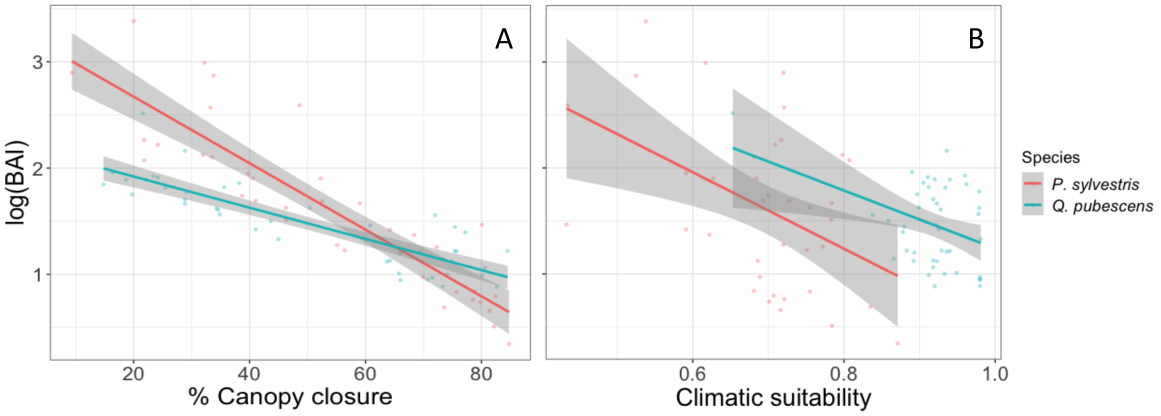

Figure 4: A: Relationship between predicted BAI and canopy closure (%) for *P. sylvestris* and *Q. pubescens*. B: Relationship between predicted BAI and climatic suitability. Both relationships were obtained from the climatic suitability-based GLM (First GLM).

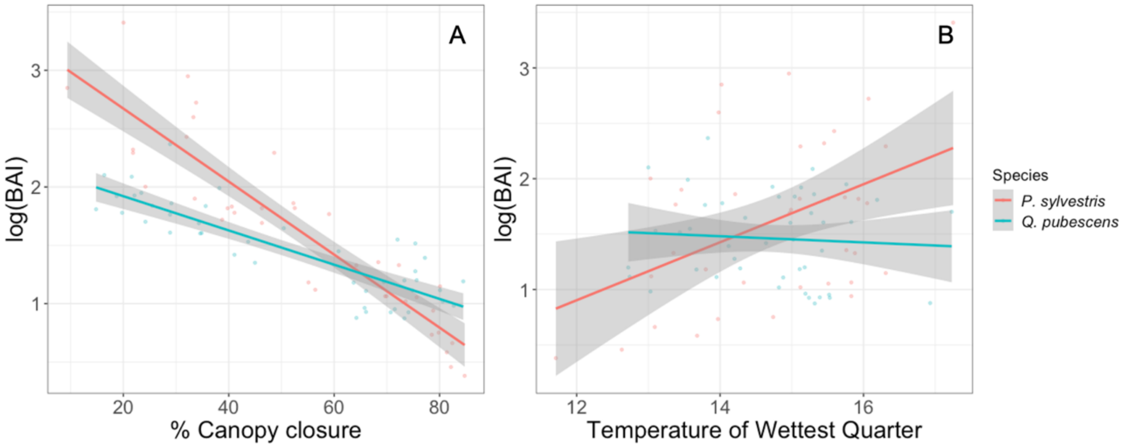

Figure 5: A: Relationship between predicted BAI and canopy closure (%) for *P. sylvestris* and *Q. pubescens*. B: Relationship between predicted BAI and Temperature of the Wettest Quarter. Both relationships were obtained from the climatic variables-based GLM (second GLM).

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).

4.4. Discussion

4.4.1. *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.

4.4.2. 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*.

4.4.3. 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).

4.4.4. 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).

4.5. 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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Supplementary material

Chapter 4

Table S1: Table of some characteristics of the studied trees and micro-site conditions where they live. The meaning of the following column names is: *Id*: Identification tree code. *Canopy type*: Type of *Pinus* canopy above the studied tree. *Slope*: Degree of slope of the 5 nearest meters of the tree in terms of % (meters/meters*100.). *Perimeter*: tree perimeter in centimeters (cm.). Geographic Coordinates are represented in decimal longitude and latitude with WGS84 reference system (Long. (º) Lat.(º)). CS: species Climatic suitability for each site.

Id	Especies	Canopy type	Slope (%)	Perimeter (cm)	Long. (º)	Lat. (º)	CS
1	*Quercus*	Dead	11	35	1,10445868	42,3494812	0,890
2	*Pinus*	Dead	20	28,4	1,10268138	42,3492357	0,866
3	*Quercus*	Green	23	27,8	1,10325437	42,3495604	0,859
4	*Quercus*	Dead	35	26,4	1,10474714	42,3503866	0,897
5	*Pinus*	Green	23	29,6	1,10409501	42,3510782	0,880
6	*Pinus*	Green	26	32	1,10396613	42,350923	0,912
7	*Quercus*	Dead	24	27	1,10265636	42,3508743	0,923
8	*Pinus*	Dead	26	44,8	1,10229627	42,3515438	0,905
9	*Quercus*	Green	28	46	1,10196889	42,3515293	0,920
10	*Pinus*	Dead	31	59,8	1,10177744	42,3514361	0,838
11	*Pinus*	Green	36	25	1,09654514	42,3437756	0,928
12	*Pinus*	Green	34	29	1,09573038	42,3434198	0,920
13	*Pinus*	Green	32	23	1,09507391	42,3430487	0,923
14	*Quercus*	Green	38	28,2	1,09297728	42,3429328	0,980
15	*Pinus*	Green	26	25,2	1,09248779	42,3442665	0,980
16	*Quercus*	Green	28	25,2	1,09347736	42,3452646	0,978
17	*Quercus*	Dead	34	45,3	1,09360006	42,3452216	0,981
18	*Pinus*	Green	19	49,2	1,09365975	42,3448533	0,979
19	*Quercus*	Green	18,5	25,1	1,0940514	42,3443465	0,979
20	*Pinus*	Dead	20,4	24,3	1,09412192	42,344825	0,980
21	*Quercus*	Green	43	46	1,0884778	42,3463971	0,980
22	*Pinus*	Green	25	25	1,08918144	42,3476155	0,918
23	*Pinus*	Green	36	29,8	1,08942658	42,3475386	0,918
24	*Quercus*	Dead	40,95	31,9	1,08956728	42,3469015	0,929
25	*Quercus*	Dead	28,8	37,8	1,08964717	42,3466687	0,878
26	*Pinus*	Dead	29,7	31,9	1,08996347	42,346647	0,960
27	*Quercus*	Dead	45	30,7	1,0880099	42,3458129	0,911
28	*Pinus*	Dead	35	21,9	1,08799137	42,3456235	0,940
29	*Pinus*	Dead	30,4	55,5	1,0990531	42,3636746	0,934
30	*Quercus*	Green	36,2	24,2	1,09884222	42,363419	0,933

Table S1. **Extended**

Id	Especies	Canopy type	Slope (%)	Perimeter (cm)	Long. (º)	Lat. (º)	CS
31	*Pinus*	Dead	30,6	51,4	1,09954375	42,3635117	0,653
32	*Pinus*	Dead	25,65	21,9	1,09883551	42,3632388	0,922
33	*Quercus*	Green	30,6	27,4	1,09867021	42,3630829	0,936
34	*Pinus*	Dead	21,4	25,2	1,09779649	42,3622579	0,940
35	*Quercus*	Dead	22,64	34,1	1,09762712	42,3622371	0,949
36	*Pinus*	Green	33,5	22,7	1,09643804	42,3618031	0,883
37	*Quercus*	Green	31,3	28,8	1,09648877	42,3617319	0,892
38	*Quercus*	Dead	29,34	41,4	1,09641495	42,3613614	0,899
39	*Quercus*	Dead	32,4	36,8	1,09649212	42,3612186	0,893
40	*Quercus*	Green	36	22,6	1,09619567	42,3613848	0,912
41	*Pinus*	Dead	39	22,8	1,0960282	42,361301	0,962
42	*Pinus*	Green	14,94	35	1,09555469	42,3608969	0,925
43	*Pinus*	Green	25,52	26,6	1,09368703	42,359614	0,918
44	*Quercus*	Green	41,63	25,8	1,09298475	42,3595483	0,936
45	*Pinus*	Green	13,41	34,2	1,09246381	42,3591074	0,709
46	*Pinus*	Green	33,66	27,9	1,0919752	42,3588021	0,708
47	*Quercus*	Green	24,62	25,6	1,09011314	42,3581407	0,707
48	*Pinus*	Dead	36,45	65	1,09015064	42,3581053	0,720
49	*Quercus*	Dead	31,99	32,3	1,08996805	42,3581202	0,721
50	*Quercus*	Green	24,84	38,6	1,08823455	42,348014	0,784
51	*Pinus*	Dead	29,25	43	1,08780153	42,3478807	0,871
52	*Pinus*	Green	14,36	26,8	1,0880265	42,3476683	0,736
53	*Pinus*	Dead	42,17	29	1,08850969	42,3477484	0,750
54	*Pinus*	Dead	16	27,9	1,08896643	42,3479001	0,772
55	*Quercus*	Green	35,1	44,4	1,09159613	42,3468543	0,751
56	*Pinus*	Dead	31,545	31,9	1,09384454	42,3576174	0,701
57	*Pinus*	Green	25,65	30	1,09433206	42,3579587	0,686
58	*Quercus*	Dead	33,39	43,8	1,09517372	42,3582339	0,681
59	*Quercus*	Dead	43,79	39,4	1,09586658	42,3582094	0,720
60	*Quercus*	Green	45,9	39,4	1,09600652	42,3571941	0,525
61	*Pinus*	Dead	26,15	22	1,09624173	42,3570449	0,435
62	*Pinus*	Dead	24,57	28,3	1,09350126	42,356522	0,693
63	*Quercus*	Dead	41,27	37,2	1,09339013	42,3565832	0,627
64	*Quercus*	Green	31,05	26,6	1,08263042	42,3490551	0,689
65	*Quercus*	Dead	33,75	46,9	1,08242414	42,3490517	0,591
66	*Quercus*	Green	34,34	40,9	1,08279529	42,3488237	0,433
67	*Pinus*	Green	30,06	28,2	1,08281983	42,3488151	0,605
68	*Quercus*	Green	26,51	34,7	1,08292904	42,348817	0,622
69	*Quercus*	Dead	41,72	37,2	1,08244521	42,3483586	0,591
70	*Quercus*	Green	31,725	23,1	1,08246957	42,3487552	0,538

Table S1. **Extended**

Id	Especies	Canopy type	Slope (%)	Perimeter (cm)	Long. (º)	Lat. (º)	CS
71	*Pinus*	Green	33,75	40,4	1,08124254	42,3483835	0,798
72	*Pinus*	Green	31,41	26,3	1,08387327	42,3465093	0,681
73	*Quercus*	Green	30,32	40,5	1,08373013	42,3464258	0,783
74	*Quercus*	Dead	22,28	30	1,08410536	42,3460629	0,807
75	*Quercus*	Dead	27,45	40,7	1,08541965	42,3459588	0,755
76	*Pinus*	Green	29,93	26,6	1,08637331	42,3461368	0,755
77	*Pinus*	Dead	24,89	40,7	1,09450419	42,3566828	0,700
78	*Pinus*	Green	26,69	45,3	1,09444134	42,3567538	0,717
79	*Quercus*	Green	45,5	28,4	1,09415197	42,3566859	0,835
80	*Quercus*	Dead	41,4	42,2	1,09411257	42,3567843	0,834
81	*Quercus*	Dead	35,5	34,3	1,09148279	42,3586228	0,701
82	*Pinus*	Dead	18,19	54	1,09336979	42,3452087	0,721
83	*Pinus*	Dead	51,75	69,3	1,08514281	42,3470799	0,728
84	*Quercus*	Dead	31,19	26,3	1,08514281	42,3470799	0,728
85	*Pinus*	Dead	24,89	46,7	1,08686959	42,3457849	0,784
86	*Pinus*	Green	33,75	24,5	1,08621315	42,3454137	0,617
87	*Quercus*	Green	20,84	32,8	1,0869437	42,3473441	0,684
88	*Quercus*	Dead	33,75	57,5	1,09079202	42,3477505	0,716

Table S2: BRT evaluation and mean outputs for our studied plots. The following headers abbreviations mean: N= number of presences used to build the BRT model. AUC = mean values of the AUC (evaluation method used). Cor = correlation coefficient of the model. CS = mean Climatic suitability for each species in all studied plots. BIO 1 = mean annual temperature of the studied plots. BIO 8 = Mean temperature of the wettest quarter. BIO 9 = mean temperature of the driest quarter. All the temperature variables are in Celsius degrees.

Species	*N*	*AUC*	*CS*	*Cor.*	*BIO 1 (º)*	*BIO 8 (º)*	*BIO 9 (º)*
Pinus	10,383	0.90	0.7±0.094	0.72	12.04±1.02	14.65±1.29	3.94±0.48
Quercus	2,556	0.92	0.92±0.054	0.77	12.24±1.18	14.70±1.04	4.20±1.04

Table S3: Results of post-hoc Tukey pair-wise comparisons from the two-way ANOVA.

Comparision	**Difference**	**Lwr.**	**Upr.**	***p* adj**
***P. sylvestris*:Defoliated canopy –** ***P. sylvestris* : Green canopy**	1.50268	1.00151	2.00385	<0.00001
***Q. pubescens*:Defoliated canopy –** ***Q. pubescens*: Green canopy**	0.62985	0.13403	1.12567	0.00696
***Q. pubescens*:Defoliated canopy –** ***P. sylvestris*: Defoliated canopy**	-0.30189	-1.42164851	-0.4418573	0.00002
***Q. pubescens*:Green canopy –** ***P. sylvestris*: Green canopy**	0.57092	0.07510	1.06670	0.01739
P. sylvestris – Q. pubescens	0.13903	-0.1281	0.40626	0.30376
Defoliated canopy – Green canopy	1.0568	0.78957	1.32403	<0.00001

Table S4: Estimates for the Linear Model used to relate Climatic Suitability and elevation. Climatic suitability of the given species was used as the response variable and Elevation (meters, m.) was the explanatory. Both *p* value of the explanatory variable an r squared were also included.

Species	**Intercept**	**Elevation**	***p (Elevavtion)***	**r^2**
Pinus	0.4209	2.9170	0.00005	0.38
Quercus	1.0350	-0.0001	0.00196	0.21

Table S5: Estimates of the LM used to relate Temperature of the Wettest Quarter (Response variable) with both explanatory variables plot type (green canopy vs defoliated canopy) and elevation (m.).

Variable	**Estimate**	***p***
Intercept	19.1879	<0.00001
Elevation	-0.00482	<0.00001
Plot type [Defoliated canopy]	0.30344	0.01060

Chapter 5

General discussion

5.1. Climatic suitability and resilience

5.1.1. Historical and event climatic suitability

Climatic suitability indices derived from species distribution models (SDMs) can overall explain both short-term recovery and medium-term dynamics (chapter 3) in forests responding to climatic extreme events. We examined the relevance of these indices at regional scale in the metropolitan France extension for several species shortly after an intense extreme episode (chapter 2), and also at population-level during a longer lapse (chapter 3). These studies show how historical climatic conditions, translated to climatic suitability (HCS), can overall modulate resistance and recovery of forest populations. Specifically, we found that the interaction between the historical climatic conditions experienced by populations and the climatic suitability during a particular extreme climatic event (ECS) had a relevant role in determining forest response to extreme drought, likely associated to climate change. These results are in accordance with previous research (Lloret & Kitzberger, 2018) and indicate the adequacy of the climatic derived SDMs indices to capture the severity of a given extreme event (Pérez Navarro et al., 2018) and also to standardize the event intensity in relation to the historical climatic conditions that species and populations experienced (Lloret & Kitzberger, 2018; Sapes et al., 2017). Further, our novel findings highlight the utility of these indices when considering different species with diverse traits and niche characteristics that experienced unfavourable climatic events across regional scale (chapter 2).

5.1.2. Climatic suitability variability

The variability of the climatic conditions that a given population has historically experienced before the climatic extreme event (HCS-SD) also plays a relevant role, at least at regional scale, on the resistance in front of episodes of hot-droughts (chapter 2). Our study reveals that populations that had experienced large climatic variability were more resistant to die-off than populations located in sites with more stable historical climate. This relationship between (HCS-SD) and resistance to die-off seems to be significant for many species. This pattern is concordant with other studies emphasizing the resilience capacity of ecosystems that historically have experienced more frequent disturbances regime (Seidl, Rammer, & Spies, 2014). Althought, we didn't elucidated how the role of past climatic variability may also support the idea that the present resistant populations would not have enough future recovery capacity against new disturbances (Anderson-Teixeira et al., 2013; Johnstone, McIntire, Pedersen, King, & Pisaric, 2010) in future climate change scenario (Spinoni, Vogt, Naumann, Barbosa, & Dosio, 2018), making unsuitable current localities for some species (Buma & Wessman, 2013; Stevens-Rumann et al., 2018). The results overall reveal that the consideration of historical climatic variability as an explicative variable is needed to understand how climatic variability could modulate community resilience and it should be incorporated in modelling exercises of vegetation responses to both climate changes scenarios and climatic extreme events. Recent works (see Elvira et al., 2021; Perez-Navarro et al., 2021) are already considering interannual climatic variables, in addition to climatic averages, when characterizing the species climatic niche space, and exploring the relationship the location of populations and communities within this space to their response to climatic and biotic disturbances.

5.1.3. Spatiotemporal trends of forest dynamics related to climatic suitability

We found that the recovery (engineering resilience) in *Pinus sylvestris* populations living in the species's geographic edge of distribution can be modulated by their expected medium-term future climatic suitability trends. Our simulation projections point out to a loss of resilience at medium-term due to the depletion of the species s climatic suitability provoked by an increase of temperature induced by climate change (chapter 3). This relationship between resilience loss and climate change scenario is due to the correlation between climatic suitability and the internal processes of the populations -i.e., vital rates- for which demographics models (IPMs) are built. The greater resilience capacity in a hypothetical constant future climate scenario in comparison to a climate change scenario, is explained by the positive correlation between climatic suitability and both seedling's establishment and growth of the remaining trees. These findings also emphasize the likely greater recovery capacity in locations with more historical climatic suitability (HCS). However, the recruitment rate of adult trees (i.e., ingrowth) seems to be negatively related to climatic suitability. Nevertheless, IPMs integrate the different vital rates and the outcome show a resilience loss at medium-term with climate change (RCPs 4.5 and 8.0 carbon scenarios) in spite of the existence of medium-term recovery even in these harsher scenarios. The study reveals that predictions of populations performance at landscape and medium-term scale may gain from considering the relationship between climatic indices derived from SDMs and some population demographic rates. Further, as said before, these indices can also describe short-term populations response at regional scale (chapter 2), highlighting the utility of theses indices when studying populations response across different spatiotemporal scales.

We observed that pioneer species *Pinus sylvestris* resilience facing extreme events also occur when we scaling down the study observation at micro-local level. Patterns of self-replacement are observed in stands affected by die-off previously dominated by *Pinus sylvestris* but with other accompanying tree species (*Quercus pubescens*) in the understory. This *Pinus* self-replacement occurs despite low climatic suitability of this studied tree species at such location (chapter 4), but the relationship between micro-local climatic suitability obtained from SDMs appears elusive. This fact highlights the importance of variables that act locally and individually - i.e., operating at scale of meters-, such as competition, micro-local environmental conditions and site-quality when assessing resilience at this spatial scale.

To summarize, we found a relationship between derived indices of SDM and some demographic variables of the population (seedling establishment, seedlings survival and growth). Our findings indicated that those climatic indices could contribute to predict populations' performance at different relatively large spatiotemporal scales (i.e. from landscape to region) (chapter 2 and 3). However, populations' response facing extreme events at smaller scales could not be easily explained by SDMs derived indices even when considering coexisting species with distinct climatic characterization (chapter 4). Thus, resilience and future populations projections are not sound enough, when focusing on micro-local and individual patterns (chapter 4), due to other sources of micro-local variability (Jofre Carnicer et al., 2021), which are very difficult to capture when using SDMs, based on regional species distribution patterns.

5.2. Forest structure and resilience

5.2.1. Basal area and understory

At small spatial scale, forest structure plays an important role in resilience. We observed that large gap openings due to the die-off-induced loss of basal area favored the growth of understory trees, regardless their specific climatic suitability (chapter 4). Further, it was also observed a negative relationship between stand basal area and both future growth and seedlings establishment, as expected in pioneer and shade-intolerant species (Kara & Topaçoğlu, 2018; Yamamoto, 2000). The growth of understory trees belonging to the previously dominating species can be favored by higher light incidence and the release of competence, even when the local climatic conditions of that location are poorly suitable (low HCS) for these species (chapter 4). This enhancement of understory trees suggests that the canopy self-replacement of the dominant established species in micro-local die-off gaps could happen at short-term when other species with more climatic suitability were not previously established at the same gap.

Resilience - in terms of recovery - at local level can be explained by mechanisms related to forest structure. In our study cases (chapter 3, 4), stands generally dominated by *Pinus sylvestris* can be resilient and persist thanks to structural changes in the community provoked by the die-off process. These die-off episodes can break natural succession - stopping the transition to closer canopies of *P. sylvestris-,* therefore preventing the establishment of more shade-tolerant species such as *Quercus spp.* Pioneer species strategies include light tolerance and further growth during juvenile stages (Brzeziecki & Kienast, 1994; Whitmore, 1989), so self-replacement of these pioneer species, such as *P. sylvestris,* can be favored due to the creation of gaps by drought-induced die-off. Tree mortality can provoke a reduction of basal area and stand density, inducing a release of competence. We hypothesized that after a die-off event, the remaining individuals of populations located near their realized climatic niche edge can persist even under lower climatic suitability conditions, since they could indeed be located within their fundamental niche, that is in sites with climatic conditions allow the species to persist, regardless biotic interactions. This persistence and self-replacement of dominant tree species under unfavorable conditions - corresponding to areas in a climatic space sited between the realized and the fundamental niche edges- can be attained by changes in forest structure, promoting a reduction of negative biotic interactions, such as competence.

To summarize, changes in forest structure at local scale, like competition suppression and the creation of new micro-local conditions provoked by the canopy openness could favor resilience of pioneer species previously affected by die-off, and this may happen even in locations with poor suitable conditions. This resilience and persistence of the populations can be enhanced especially in stands with management legacies, such as historical suppression of accompanying species. All of these processes may make the realized niche wider and therefore diluting the differentiation between realized and fundamental niche.

At medium spatial scales (landscape-level scale), forest structure can also modulate forest resilience. We found that stands poor resistant to die-off - with high rates of basal area loss – will recover their structure at least half a century after the drought-induced disturbance (chapter 3). Changes in forest structure due to die-off provoked a competence release and higher insolation levels in the understory, thus enhancing resilience mechanisms that promotes regeneration and growth of surviving trees. That is, structural changes induced by die-off augmented the growth of the remaining trees, seedling establishment and survival probability of individuals across time (chapter 3). Nevertheless, when comparing future projections of stands structure 50 years after the episode, we observed that unaffected stands still show higher basal area than previously die-off affected stands, likely due to the loss of basal area during the drought event (chapter 3).

At larger spatial scales, the relationship between resilience and forest structure tends to be diluted (chapter 2). We found that basal area and stand density are not overall good predictors of short-term resilience to the drought event, in contrast to other studies (Bottero et al., 2017; Palareti et al., 2017). Nevertheless, the role of basal area and stand structure appears again important on forest resilience at species-specific level (chapter 2). At regional scale, dense populations of some species such as *Fraxinus excelsior*, *Quercus petraea* and *Pinus pinaster* showed less resilience to die-off than sparse ones. In contrast, populations of *Quercus ilex* and *Betula pendula* tended to be less resilient in populations with less basal area. This species-specific patterns of resilience in relation to stand structure suggest that acclimatation processes (Clark et al., 2016; Tomasella et al., 2018) and species functional traits (Greenwood et al., 2017) can modulate climatic extreme specific responses at regional and continental scales.

5.2.2. Management implications

Under a water stress scenario, forest management practices, such as thinning prior to the die-off episodes, can increase population resistance enhancing tree growth and survival probability (Giuggiola, Bugmann, Zingg, Dobbertin, & Rigling, 2013; Sohn, Hartig, et al., 2016). These forest practices can simulate forest gap openings, similarly to a natural disturbance. Therefore, they can promote seedlings establishment and growth of the understorey trees, that is, resilience-related stabilizing mechanisms in front of die-off (chapter 3 and 4). Importantly, regeneration success would eventually be determined by the type of forest thinning, soil preparation practices, and the timing of the management activities (Barbeito, Lemay, Calama, & Cañellas, 2011).

By the other hand, in no-managed stands the establishment of other accompanying species, which may be more shade-tolerant (chapter 4) can reduce resilience. In fact, forest canopy tends to favour the local maintenance of less suitable species under climate change (Zellweger et al., 2020). These species, often related to more mature stages in forest succession, could be challenged in new environments with more die-off events leading to the loss of canopy closure. In addition, replacement by other species is also dependent of dispersal, or alternatively presence in the stands. Both processes, in turn, are usually determined by forest management legacies (Bobiec, Jaszcz, & Wojtunik, 2011; Máliš et al., 2021).

5.3. Future research

This thesis has demonstrated that the use of climatic suitability indices can explain forest resilience facing climatic extreme events. However, there is an important variability of this response at both regional and multi-specific scales. Globally, the deviance explained using this approach can also be low. An important source of uncertainty is due to the intrinsic variability of climatic conditions in a given site. Therefore, improved procedures are needed to capture such climatic variability of the conditions in which species live. Some recent studies have developed climatic suitability indices based on climatic environmental spaces built from yearly bioclimatic variables instead climatic averages. The results have shown that this procedure, based on calculate the distances between the location in the environmental space of the conditions in a given site ant the optimum or the edge of the species climatic niche - envelope - , allows to capture properly the recovery and the resistance of a given population and community facing perturbations or climatic extreme events (Elvira et al., 2021; Perez-Navarro et al., 2020). Until now, these studies have focused on populations and local levels, and it would be interesting to expand this procedure at broader scales.

In general, resilience patterns - which are inversely related to vulnerability - to die-off tend to be species-specific, but some patterns among chorological groups of species are found (chapter 2). This suggests that biogeographic-related processes such as acclimatization, adaptation, and distribution of species functional traits likely play an important role in vulnerability and resilience to extreme climatic events. Not enough research has been done on how the biology of species and their related traits may influence resilience. It would be interesting to investigate how strategies such as light tolerance and the successional character of the species (pioneer *vs.* late successional) will affect the persistence and resilience of populations and communities in a future context of more frequent disturbances, such as die-off episodes with the capacity to induce canopy loss.

5.4. Concluding remarks

This thesis provides evidences that SDM derived indices are useful to standardise climatic extreme events and to predict forest resilience across species, landscapes and regions. But forest structure has a relevant influence on populations resilience too. In fact, when the study resolution scale down, forest structure becomes more relevant on forest dynamics and resilience. Therefore, SDMs derived indices, interpreted as climatic suitability, coupled with forest structure are related to drought-induced forest die-off resilience across regional scales in western Europe. Event Climatic suitability (ECS) is a useful index for standardizing the magnitude of extreme climatic events. In turn, HCS-SD is useful to explain resilience and die-off vulnerability across landscapes and species, thanks to its ability to integrate short-term past climatic legacy and its biological effect on populations. The studies have also demonstrated that, although resilience and vulnerability to die-off is species-specific, some trends related to species' chorology can be found (i.e., Euro-Siberian vs. Mediterranean and Sub-Mediterranean species). SDM derived indices are also useful tool to predict resilience and forest populations dynamics at landscape scales, given that vital rates, such as seedlings establishment and tree individual growth, are related to climatic suitability in rear edge populations of *P. sylvestris*. These forests have the capacity to recover their performance after drought-induced die-off events, due to high recruitment and enhanced growth of remaining trees after such event. This enhancement is mainly induced by changes in forest structure - loss of basal area - that would cause competence release. But this recovery does not appear to be immediate and is mediated by the climatic conditions determined by climate change scenarios. Thus, resilience would diminish under scenarios that imply a reduction of the species climatic suitability in those locations. The work also found that in forests dominated by *P. sylvestris*, short-term self-replacement patterns at micro-local scales, were determined by micro-local conditions generated by the die-off itself - micro-local climate and forest structure -, regardless species climatic suitable conditions in that location. Thus, at such scale, SDM derived indices does not well predict forest dynamics.

Conclusions

Chapter 2

- At regional scale, vulnerability –lack of resistance- to forest die-off following a hot-drought can be predicted by using SDM outputs interpreted as climatic suitability indices across regional scales.
- The climatic condition that a given population experience during a climatic extreme event standardized using SDMs, represented as Event Climatic Suitability index (ECS) is a useful tool to assess the magnitude of the studied extreme climatic event and it enable comparisons across landscapes for distinct forest species.
- Overall, the variability of the climatic suitability that populations experienced during the historical period prior an extreme climatic event expressed as HCS-SD mediated the populations' response facing this extreme event. Overall, populations that historically experienced low climatic variability tend to have less drought induced die-off resistance.
- Niche core populations, with higher Historical Climatic Suitability (HCS), that experienced harsher conditions during the hot-drought event (Low ECS), are prone to die-off. Thus, the use of SDMs makes it possible to evaluate interactions between past (HCS, HCS-SD) and present (ECS) climatic conditions, and therefore they can assess the existence of reinforcing effects of vulnerability in niche-core and niche-edge populations.
- We also demonstrated that vulnerability to die-off is mainly species-specific, but some trends related to species' chorology emerged. Populations of Eurosiberian species are expected the less resistant in front of hot-drought. While Sub-Mediterranean and Mediterranean populations are less resistant when located in their core climatic niche due among others acclimation.

- Further research applying this methodology to mixed forests is required to scale up the use of climatic suitability indices to community level. Also, given the important role of the climatic suitability variability in the population vulnerability to die-off, more research on how climatic variability modulates vegetation responses is needed.

Chapter 3

- Simulations based on IPMs allow to analyze how current die-off events can influence future mid-term population dynamics and therefore their resilience to climate change.
- Climatic suitability derived from SDMs can explain growth and regeneration patterns in forest stands. Populations placed in more climatic suitability localities experienced both more regeneration and growth after the die-off event. Contrarily, populations with less climatic suitable conditions experienced more net ingrowth to adult trees.
- Our results show that despite of the capacity of *P. sylvestris* forests to recover its structure after drought-induced die-off events, largely due to the recruitment and growth of young trees, this recovery does not appear to be immediate.
- The effect of die-off events can remain for decades, mostly due to the loss of large trees during the drought induced die-off events, which can only be replaced by new trees after several decades.
- This reduced engineering resilience will diminish even more under climate change scenarios, when climatic suitability will diminish too. This will imply higher temperature and water stress, translated in less seedling’s abundance and diametric growth of the remaining trees.
- Our models cannot capture future die-off events related to the expected higher drought frequency at mid-term due to model limitations. Nevertheless, a more drought-resistance facing future droughts will be possible in plots previously affected by die-off due to a reduction of competence.

- One of the main resilience mechanisms that support the persistence of *Pinus sylvestris* are seedlings and saplings recruitment. Further research in seedlings and saplings survival, niche requirements and growth will be useful to predict future *Pinus sylvestris* populations' performance and survival in the region.

Chapter 4

- Self-replacement patterns after drought-induced mortality in forests dominated by *P. sylvestris* were enhanced by micro-local conditions generated by the die-off itself.
- Gap opening due to drought-induced mortality can provoke a backward in the succession, promoting the growth of the pioneer species *Pinus sylvestris* and therefore its short-term self-replacement. However, later successional species, such as *Quercus pubescens*, could replace *Pinus sylvestris* canopy in locations where that species has previously stablished in the gap.
- As expected in forest succession, the maintenance of the *Pinus sylvestris* green canopy promote both establishment and growth of understorey individuals of shade-tolerant species, such as *Quercus pubescens*.
- The difference in the performance of two studied coexisting species makes it difficult to predict long-term future changes in rear-edge forests where species with different niches concur. We expected that a short term self-replacement of *Pinus sylvestris* will be possible. However, future *Quercus pubescens* seedlings stablishment could locally promote long-term replacement.
- Climatic suitability indices extracted from SDMs fail to explain the difference of growth performance of the two studies species that have different climatic niche and different life strategies. These regional-based indices can explain demographic

processes, such as mortality and die-off effects, at equivalent spatial scales. But these indices are difficult to translate to micro-local scale, as they are not build from micro-climate, soil or biotic interactions, which operate at small spatial scale.

- Despite the low climatic suitability of the studied *P. sylvestris* population, which is located in it's the species' rear-edge distribution, these results provide evidence of mechanisms that promote the resilience of *P. sylvestris* forests, i.e., growth release after gap opening, provided the tolerance limits of the species are not exceeded.

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