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RESILIENCE OF MEDITERRANEAN FORESTS IN FRONT OF COMPOUND FIRE-DROUGHT REGIMES: THE ROLE OF THE SPECIES CLIMATIC NICHE

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RESILIENCE OF MEDITERRANEAN FORESTS IN FRONT OF COMPOUND FIRE-DROUGHT REGIMES: THE ROLE OF THE SPECIES CLIMATIC NICHE

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Abstract

In the last decades, extreme weather conditions related to climatic change coupled to changes in anthropogenic land use have enhanced the frequency and magnitude of disturbances. Specifically, changes in temperature and precipitation patterns are altering the historical regimes of wildfires and droughts, promoting tree mortality of many forests worldwide. Nevertheless, the response of forest ecosystems to compound disturbance regimes and the modifications they will undergo under climate change are still not fully understood. Through this PhD Thesis, I aim to address whether the conceptual framework of the realized climatic niche of the species can further our understanding of the response of Mediterranean tree populations to compound fire-drought disturbance regimes. For this purpose, I have used niche modelling tools to extract the climatic conditions of regenerating burned populations across Spain to compute different niche metrics representing populations' position in niche space (i.e., distances to niche optimum and edge). Then, I have analyzed the relevance of population position in niche space in determining: the density of regeneration at the regional scale (Chapter 2); the recruits' performance at individual scale (Chapter 3); and the resilience of populations in terms of recruitment, considering different tree species with contrasted regeneration strategy (Chapter 4).

In Chapter 2, I assessed whether the resilience, in terms of recruit density, of populations of *Pinus halepensis* Mill. under compound fire-drought regimes are conditioned by their position within the realized species climatic niche (i.e., distance to niche optimum and edge). The climatic niche of *P. halepensis* was characterized by considering their populations across its Spanish distribution range. I found a high variability of post-fire resilience across the studied sites (Catalonia and Valencia community; NE Spain). Generalized linear models (GLM) indicated a positive relationship between fire severity and the density of *P. halepensis* regeneration. Warm conditions before the fire were positively related to pine regeneration and this effect increases under higher-severity fire. On the contrary, warm temperatures after the fire negatively affected the density of recruiting pine trees, whereas wet conditions after the fire enhanced it. Such results highlight the importance of climatic variability (measured as position in the climatic niche) prior to and after the wildfire on the regeneration response of the *P. halepensis* populations.

In Chapter 3, I used the climatic niche characterization to identify how post-fire climatic conditions and microsite characteristics modulated the performance of *P. halepensis* individuals after fire, in terms of plant size. Species' climatic niche was characterized from its European-wide distribution, crossing occurrence localities with the respective yearly values of twelve bioclimatic variables. I sampled, measured and aged newly established individuals across Catalonia (NE Spain) in forests that burned between 2002-2013. Then, I modelled plant height, basal area, crown diameter and green canopy in relation to position in niche space (i.e., metrics indicative of distance to niche optimum and edge). As expected, height, crown diameter and basal area were positively correlated with age. Plant height was higher in plants located more distant from the dry edge of the climatic niche, although years with extremely dry conditions appeared positively correlated with recruits' height. Microsite characteristics such as stoniness and the presence of surrounding *P. halepensis* cover also modulated the recruits' performance. The study reveals that position within the climatic niche, together with microsite conditions, is a useful tool to understand recruits' performance and thus post-fire regeneration patterns of *P. halepensis.*

In Chapter 4, I analyzed the post-fire regeneration of three dominant tree species in the Mediterranean Basin with contrasted regenerative strategies, *P. halepensis* (seeder), *Quercus ilex* L. (resprouter) and *Pinus nigra* J.F.Arnold (fire-sensitive), in relation to populations' position in their respective climatic niche. Using the European occurrences and the same bioclimatic variables as in Chapter 3, I characterized the climatic niche of each species and determined the wet and the dry edges of the niche. Using the Spanish National Forest Inventory (IFN), I modelled species short-term resilience across Spain, including changes in species dominance (species shift) and the recovery of canopy cover (comparing the IFN2 with the IFN3), in relation to the position of burned sites within the niche before and after the fire (i.e., distance to niche optimum and to the wet and dry edges). I also included fire severity as explanatory factor in the models. Species shift was higher in plots formerly dominated by *P. nigra*, a species without a fire-prone regenerative strategy, than in the plots dominated by the other two species. Also, fire severity significantly explained the shift of dominant species in *P. nigra* and *Q. ilex* plots, but not in *P. halepensis* ones, supporting the notion that this species is well adapted to stand-replacing wildfires. Overall, the analysis reveals that pre- and post-fire climatic

position of populations in the climatic niche, together with fire characteristics, modulates their short-term resilience to fire.

The studies of this PhD Thesis reveal that the position within the realized climatic niche of the species (i.e., distance to niche optimum and edge) offers a suitable framework to understand post-fire regeneration patterns in Mediterranean trees across different species and spatial scales. This technique is particularly useful when assessing drought-related conditions, such as the warmest quarter period (i.e., summer) or when delineating meaningful sections of the niche edge (i.e., wet and dry edges). Additionally, fire severity and micro-site characteristics also influence the post-fire response, including recruits' density and performance of populations. The insights gained in this PhD Thesis have important implications to better anticipate the response of Mediterranean populations to future compound regimes of wildfires and drought under the ongoing, global climate change.

Resumen

En las últimas décadas, las condiciones climáticas extremas relacionadas con el cambio climático, unidas al cambio en los usos antropogénicos del suelo, han incrementado la frecuencia y magnitud de las perturbaciones. Específicamente, los cambios en los patrones de temperatura y precipitación están alterando los regímenes históricos de incendios forestales y sequías causando la mortalidad de muchos bosques en todo el mundo. Sin embargo, la respuesta de las poblaciones a los regímenes compuesto de perturbaciones y las modificaciones que estos sufrirán bajo el cambio climático aún no son completamente entendidos. A través de esta Tesis Doctoral, pretendo abordar si el nicho climático realizado de la especie podría explicar la respuesta de las poblaciones de árboles mediterráneos a perturbaciones compuestas, como incendios forestales y sequías. Para este propósito, he utilizado herramientas de modelado de nicho para extraer las ubicaciones climáticas donde las poblaciones quemadas a lo largo de España se regeneran, obteniendo diferentes métricas (es decir, distancias al óptimo y el límite del nicho) que han servido para analizar: la densidad de la regeneración a escala regional (Capítulo 2); el tamaño de los reclutas a escala individual (Capítulo 3); y la resiliencia de las poblaciones en relación con su estrategia de regeneración, considerando diferentes especies arbóreas (Capítulo 4).

En el Capítulo 2, he evaluado si la resiliencia, medida como densidad de regenerado, de poblaciones de *Pinus halepensis* Mill. que han experimentado regímenes compuestos de incendios y sequías está condicionada por la posición en el nicho climático de la especie. El nicho climático de *P. halepensis* se caracterizó considerando sus poblaciones a lo largo de su distribución en España. Encontré una alta variabilidad de dicha resiliencia post-incendio en los sitios estudiados (Catalunya y Comunitat Valenciana). Modelos lineales generalizados (GLM) indicaron una relación positiva entre la severidad del incendio y la densidad de regeneración de *P. halepensis*. Las condiciones cálidas antes del incendio se relacionaron positivamente con la regeneración de pinos y este efecto aumentó bajo incendios de mayor severidad. Por el contrario, las temperaturas cálidas después del incendio afectaron negativamente la densidad de pinos, mientras que las condiciones húmedas después del incendio mejoraron la regeneración. Estos resultados destacan cómo la variabilidad climática (medida como posición en el nicho climático) antes y después del incendio influye en la respuesta regenerativa de las poblaciones de *P. halepensis*.

En el Capítulo 3, he utilizado la caracterización del nicho de la especie para estudiar cómo las condiciones climáticas posteriores al incendio y las características del microhábitat modulan el desarrollo de los individuos de *P. halepensis,* en términos de tamaño. El nicho climático de la especie se caracterizó a partir de sus registros en los inventarios forestales europeos cruzando las localidades de las ocurrencias con los respectivos valores anuales de doce variables bioclimáticas. Muestreé, medí y daté individuos de nuevo establecimiento en Cataluña en bosques que se quemaron entre 2002 y 2013. Luego, modelé la altura de la planta, el área basal, el diámetro de la copa y su porcentaje de verde en relación con las métricas del nicho (distancia al óptimo y el límite). Como se esperaba, la altura, el diámetro de la copa y el área basal se correlacionaron positivamente con la edad. La altura de la planta fue mayor en los individuos ubicados más distantes del borde seco del nicho climático, aunque años con condiciones extremadamente secas se correlacionaron positivamente con la altura de los reclutas. Las características del microhábitat, como la pedregosidad y la presencia de cobertura circundante de *P. halepensis*, también determinaron el desarrollo de los reclutas. El estudio revela que la posición de las poblaciones dentro del nicho climático es una variable útil para comprender, junto con las condiciones del microhábitat, el desarrollo de los reclutas y, por lo tanto, los patrones de regeneración post-incendio de *P. halepensis.*

En el Capítulo 4, he analizado la regeneración post-incendio de tres especies arbóreas dominantes en la Cuenca Mediterránea con estrategias regenerativas contrastadas, *P. halepensis* (germinadora), *Quercus ilex* L. (rebrotadora) y *Pinus nigra* J.F.Arnold (sensible al fuego), en relación con la posición de las poblaciones en su respectivo nicho climático. Utilizando las ocurrencias en Europa y las mismas variables bioclimáticas usadas en el Capítulo 3, caractericé el nicho climático de cada una de las especies y determiné el borde húmedo y seco de su nicho. Utilizando el Inventario Forestal Nacional (IFN) español, modelicé la resiliencia a corto plazo, incluyendo cambios en la dominancia de las especies y la recuperación de la cubierta vegetal (comparando el IFN2 con el IFN3), en relación con la posición en el nicho de las parcelas antes y después del incendio. También incluí la severidad del fuego como factor explicativo en los modelos. El cambio de especies después del fuego fue mayor en las parcelas dominadas por *P. nigra,* una especie sin una estrategia regenerativa adaptada al fuego. Además, la severidad del fuego explicó el cambio de dominancia en bosques quedamos de *P. nigra* y *Q. ilex,* pero no en *P. halepensis,* reforzando la idea de la buena adaptación de esta especie a fuegos de alta intensidad. El análisis revela que la posición climática de las poblaciones dentro del nicho climático antes y después del incendio, junto con la severidad del fuego, modula su resiliencia a los incendios.especies.

Los estudios que componen esta Tesis Doctoral revelan que la posición de las poblaciones en el nicho climático de la especie (distancia al óptimo y al límite) ofrece un marco adecuado para comprender los patrones de regeneración post-incendio en árboles mediterráneos a través de diferentes especies y escalas espaciales. Esta técnica es particularmente eficiente cuando se evalúan las condiciones relacionadas con la sequía como, por ejemplo, utilizando el período del año más cálido (es decir, el verano) o delimitando las características del borde del nicho climático (es decir, el límite húmedo y seco). Además, la severidad del incendio y las características del microhábitat también pueden influir en la respuesta post-incendio de las poblaciones. Los conocimientos derivados de esta Tesis Doctoral tienen implicaciones importantes para anticipar mejor la respuesta de las poblaciones mediterráneas a los nuevos regímenes compuestos de incendios forestales y sequía en la situación actual de cambio climático global.

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Chapter 2:

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Chapter 3:

Elvira, Nuria J.; Lloret, Francisco; Margalef-Marrase, Jordi; Díaz Borrego, Raquel & Batllori, Enric (Under review, major revision). Position in the climatic niche modulates post-fire performance of Pinus halepensis regeneration. *Forest Ecology and Management.*

Chapter 4:

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Other articles as a result of collaborative research during my PhD period.

Díaz-Borrego, Raquel; Pérez-Navarro, Maria Ángeles; Jaime, Luciana; Elvira, Nuria J. & Lloret, Francisco (2024). Climatic disequilibrium of recruit communities across a drought-induced die-off gradient in Mediterranean shrubland. *Oikos*, (7), e10465. https://doi.org/10.1111/OIK.10465

Chapter 1

Introduction

1.1 Wildfire-drought compound disturbance regime

Disturbances are considered as discrete events that modify the structure, function or composition of communities and ecosystems through mortality or damage to a part of the populations (White & Pickett, 1985). Natural disturbances can be abiotic (fire, drought, wind, ice and snow) or biotic (insects or pathogens) and are an integral part of the dynamics of terrestrial ecosystems, particularly of forests (Seidl *et al.*, 2017). Disturbance regimes are characterized by multiple components including frequency, intensity, severity, seasonality or size of the affected area, as well as their interactions (Davies *et al.*, 2009; Turner, 2010). Additionally, the different disturbance agents can interact with each other. Indeed, compound disturbance regimes can have a more profound impact on ecosystems than the influence of disturbances acting alone (Batllori *et al.*, 2019; Buma, 2015), and the timing, sequence and number of disturbance events are critical to ecosystem response. Direct effects of disturbances acting in isolation have been widely studied, but indirect effects and compound disturbances regimes need more attention, especially in the context of climate change under which novel disturbance outcomes are likely to arise from altered disturbance interactions (Turner & Seidl, 2023).

Of the disturbances that are affecting the Earth's forest ecosystems, fire is among those that have the greatest influence on vegetation patterns and dynamics (McDowell *et al.*, 2020). Wildfires are one of the main shapers of forest ecosystems around the world, modifying the structure and composition of vegetation, at the landscape and global scales (Bond *et al.*, 2005; McDowell *et al.*, 2020; Whelan, 1995). The fire regime is composed of the magnitude of the combustion (fire intensity), the damage it produces to the vegetation (fire severity), the spatiotemporal distribution that determines the extension of the fire (burned area), and the frequency, return time and seasonality of fires, being all these components interconnected (Keeley, 1995; Moreira *et al.*, 2011; Viana-Soto *et al.*, 2017). Wildfires have acted as an evolutionary force that, in fire-prone systems such as Mediterranean forests and shrublands, have conditioned the physiology and reproductive traits of species which allow them to survive or recover following fires (Beckage *et al.*, 2009; Keeley, Pausas, *et al.*, 2011; McLauchlan *et al.*, 2020). Some of the most adaptive traits in fire-prone ecosystems include fire-stimulated flowering, canopy seed storage (serotiny), fire-stimulated germination, bud protection, and sprouting (Gill, 1977; Lamont & He, 2017). The presence and combination of these traits determine the dynamics (i.e., the resilience) after wildfires of fire-prone ecosystems, such as Mediterranean ones (Enright *et al*., 2014).

Fire interaction with other disturbance agents such as wind or drought can modify the characteristics of the variables that compose fire regimes and, therefore, the effects of wildfires upon ecosystems. The weather conditions that directly affect fire behaviour are known as fire weather (e.g., fire ignition, intensity and propagation are exacerbated by strong winds, high temperatures, and low humidity, Pausas & Keeley, 2021). For instance, in wind-driven fires wind can compensate or offset other factors, by changing the direction of the propagation and determining the intensity, thus modifying the shape, size and duration of the fires (Pausas & Keeley, 2021). Droughts, on the other hand, that are also driven by some fire weather components (e.g., precipitation, temperature), and, in turn, increase the amount of dead fuel and decrease the water content of vegetation, which likely increases the frequency and intensity of fires (Aldersley *et al*., 2011; Liu *et al*., 2010). In woody-dominated ecosystems, drought also increases fuel connectivity (horizontal and vertical) by promoting the mortality of the vegetation.

In the context of global change, climate modifications could significantly affect forest disturbance regimes at the regional and global scales (McDowell *et al*., 2020; Seidl *et al*., 2017). These changes can be especially relevant in regions such as the Mediterranean Basin, since, according to climate change projections, higher temperatures and lower rainfall are expected, especially in summer (IPCC, 2014, 2023; Ozturk *et al*., 2015; Spinoni *et al*., 2018). Climate and land use change increase the frequency of confluence of wildfire drivers (e.g., appropriate fire weather conditions, amount and continuity of fuel), increasing fire intensity, the number of dry years and extending the duration of the fire season, and, thus, the number of days with high weather fire risk (Colantoni *et al*., 2020; Pausas & Keeley, 2021). In turn, land abandonment in the last decades in many temperate regions and the consequent encroachment and afforestation increases fuel load and its continuity across the landscape (Colantoni *et al*., 2020). Also, the human management of fires and landscapes can modify fire behaviour. In temperate and Mediterranean forests, fire suppression policy tends to favour understory vegetation resulting in vertical connectivity which increases the likelihood of high-intensity crown fires (Alvarez *et al*., 2024; Covington & Moore, 1994; Curt & Frejaville, 2018; Pausas & Fernández-Muñoz, 2012; Pausas & Keeley, 2021; Swetnam *et al*., 2016).

Under the current climatic conditions, the compound regime of drought and fires acquires special relevance since higher temperatures and precipitation variability are leading to more frequent and intense episodes of drought (hotter droughts; Allen *et al*., 2015). Additionally, the impacts of drought are expected to further increase in frequency, intensity and length in the next decades (Ploughe *et al*., 2019; Smith, 2011). In turn, pre-fire and post-fire drought conditions may reduce seed production, resprouting success or seedlings survival (Parra & Moreno, 2018; Werner *et al*., 2022), thus, impacting the resilience capacity of ecosystems (Henzler *et al*., 2018).

The Mediterranean bioclimatic regions show high inter-annual variability but overall are characterized by seasonally low precipitations during the period with the highest annual temperatures (i.e., summer). Species are thus adapted to seasonal drought (e.g., resulting in sclerophyll vegetation). In addition, the alternation of mild and productive seasons (spring, autumn), when biomass accumulates, with dry and hot summers, that promote fires, makes Mediterranean-type ecosystems a paradigmatic example of fire-prone vegetation. On the other hand, the Mediterranean Basin is considered a biodiversity hotspot (Myers *et al*., 2000) with a great diversity of habitats where a high number of endemism co-exist in a transitional zone between semi-arid and temperate climates (Palahi *et al*., 2008; Solomou *et al*., 2017). Thus, in Mediterranean-type ecosystems, the predominance of evergreen sclerophyllous trees and shrubs is a common feature (Bussotti & Pollastrini, 2020). Evergreen pines and oaks commonly coexist in Mediterranean forests, in many cases forming monospecific forests, largely as a consequence of intense past management and exploitation (Vicente *et al*., 2018). These species show functional traits that allow them to cope with the climate and the disturbances that characterize Mediterranean-type ecosystems. Some of these traits include small, long-lived and thick leaves (i.e., sclerophyllous leaves with low specific leaf area) with strong stomatic control that reduces the evapotranspiration and enables them to survive during drought periods (Chaves *et al*., 2003), or the formation of resistance forms (e.g., lignotubers with underground buds and stored reserves, or fire-mediated seed bank) to cope with wildfires and regenerate in burned areas.

1.2 Regeneration traits and resilience.

In the broad sense, resilience refers to the ability of systems to avoid shifting to alternative states (Holling, 1973) and under a disturbance regime perspective it applies to the system's ability to remain or return to the previous state after disturbances or heavy stress (engineering resilience, Pimm, 1984). In the context of global change, resilience has become a major topic of research in ecological studies, with a focus on management actions to promote it under current environmental challenges (Cantarello *et al*., 2024; Davis & Shaw, 2001; Geng *et al*., 2019; Hodgson *et al*., 2015). In forest ecosystems, populations' ability to cope with disturbances largely depends on subsequent regeneration (Johnstone *et al*., 2016; Martínez-Vilalta & Lloret, 2016), in addition to their resistance to the direct impact of the disturbances. The mechanisms of species to restore their populations include the establishment of recruits from aerial or soil seedbanks (i.e., seeder strategy) or the regrowth from surviving, protected tissues (i.e., resprouting strategy) (Davis *et al*., 2019; Ibáñez *et al*., 2019; Karavani *et al*., 2018; Pausas & Keeley, 2014). Therefore, forests dominated by tree species without a seed bank resistant to fire or that do not resprout after it, are likely to lose their composition and structure in burned areas (fire-sensitive species; Coop *et al*., 2020).

Post-fire regeneration dynamics are highly complex due to the multitude of processes that affect the establishment of individuals or the resprouting capacity, thus determining population resilience (Figure 1.1). For instance, in resprouting species, the climatic conditions before wildfire modulate the formation of the protective and storage tissues that allow them to survive and recover afterwards (Karavani *et al*., 2018; Pausas *et al*., 2018). In the case of seeder species, the climatic conditions after disturbances play a determinant role in the success of recruitment, given that seedlings are highly sensitive to climatic stress during the first years after wildfire (De Luís *et al*., 2005; Fenner, 1987). Additionally, burned areas can exhibit high erosion and seed predation rates (Broncano *et al*., 2007; Girona-García *et al*., 2021) that may constrain seed availability. At the same time, after the wildfire, newly established seedlings encounter environments with reduced competition and an increase in key resources such as light or nutrients (Marañón-Jiménez *et al*., 2013; Pausas *et al*., 2008). Therefore, successful recruitment is likely influenced by climatic components associated with drought (Baudena *et al*., 2020; Davis *et al*., 2019), which determine abiotic (i.e., dryness) and biotic drivers (i.e., ecophysiological processes and biotic interactions) of regeneration. Thus, the ability of species to regenerate after disturbances such as fires and the influence of climatic conditions on these regeneration patterns can ultimately determine the resilience of populations.

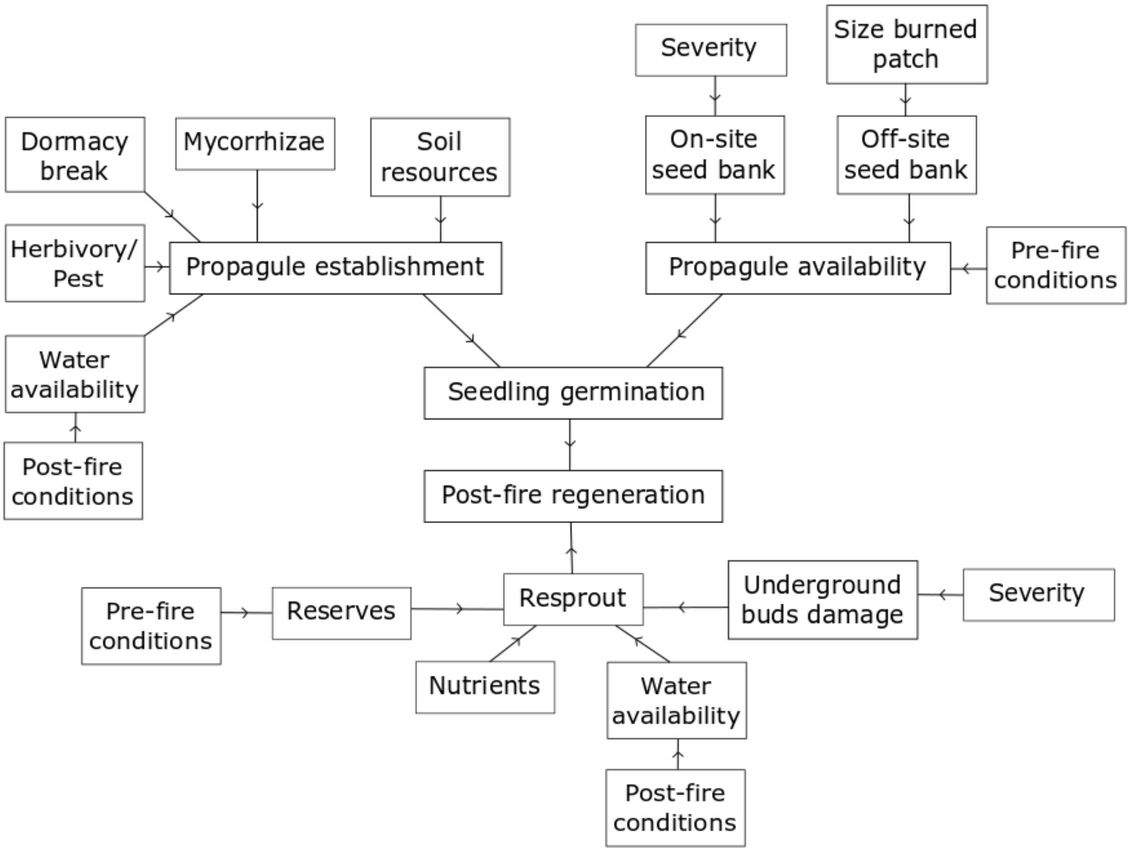


Figure 1.1: Diagram of post-fire regeneration drivers, which depend on the regeneration strategy, mediated by seedlings establishment (seeders) or resprouting ability (resprouters). A multitude of processes interact and determine stand-level resilience. Pre-fire and post-fire conditions refer here to climatic conditions, such as temperature and precipitation. Modified from Karavani *et al*., 2018.

Local-scale processes, such as soils, biotic interactions and management, are important modulating agents of regeneration success after disturbance (McLauchlan *et al*., 2020). For instance, the presence of neighbouring plants likely influences the development of recruitment through inter or intraspecies competition for resources, modifying the response of recruits to local climatic conditions (Martin-Benito *et al*., 2011; Moya *et al*., 2018; Ne'eman *et al*., 2004; Pausas *et al*., 2002). However, facilitative interactions promoting the recruitment and establishment of new individuals may counterbalance competition processes (Alcántara *et al*., 2018; Brooker, 2006; Ploughe *et al*., 2019). Plant cover implies the interaction of several variables with large effects in the initial stages of plant development (i.e., seedling occurrence and success under the canopy or in canopy gaps) (Maestre *et al*., 2003). Finally, soil properties (e.g., depth and rockiness, organic matter content) and ground cover generating microhabitats (e.g., leaf litter, decayed branches) are also relevant for recruitment success.

1.3 Species climatic niche

Climatic conditions have a key role in the regeneration and establishment of species after fires (Nolan *et al*., 2021). Following the Hutchinsonian definition of the ecological niche (Hutchinson, 1957), the climatic factors that allow the species to survive and reproduce would correspond to the climatic niche. Other factors that can limit species distributions include abiotic gradients such as soils, topography and sunlight, dispersal ability, and biotic interactions including competitors, predators, pests, pathogens and facilitators (Gaston, 2003). As opposed to the fundamental niche, which is determined by species physiological tolerances, the niche that is determined by the environmental characteristics of the geographic sites where a given species is found corresponds to the realized climatic niche, which indirectly incorporates the above-mentioned biotic interactions (Carscadden *et al*., 2020; Peterson, 2011). Within the n-dimensional space corresponding to the niche, it is assumed that a gradient exists from locations where the species perform best (niche optimum, core or centroid) to adjacent space where species fitness gradually decreases towards a boundary with suboptimal conditions (niche limit, edge or margin). Therefore, it is assumed that the demographic rates of species within their niche are different at each site within the n-dimensional space (Brown, 1984; Hutchinson, 1957). This assumption is a widely used paradigm in biogeography, that translating the environmental niche space to the geographical one, has received the name of the Centre-Periphery Hypothesis (CPH, Brown, 1984; Hengeveld & Haeck, 1982; Pironon *et al*., 2018). This hypothesis predicts that the fitness of species decreases progressively from the centre of geographical distribution towards the margins.

Within the niche framework, and from the perspective of a given species, climatic gradients can be translated into conditions being closer to the niche optimum or the niche edge of the species. So, ultimately, species would not persist beyond the niche's boundaries. However, several circumstances allow populations to temporarily exist outside the edges of the niche, both in the case of the geographical niche and the climatic niche. For instance, when a population suffers disturbances (e.g., extreme climate events), these could displace the population outside the limits of the climatic niche. In the case of extreme droughts (Pérez Navarro *et al*., 2018), which represent dry and hot conditions far from the climatic optimal for the species, the magnitude and the duration of drought will determine the effects of these disturbances on natural populations, also modulated by microhabitat effects (Díaz-Borrego *et al*., 2024). It is expected that the distance to the edge of the niche determines the demographic responses of the species, which will be better the closer they are to the niche optimum , and poorer for populations located at or beyond the niche edge (Perez-Navarro *et al*., 2022). However, the demographic responses of the species may differ from its historical pattern due to acclimation to new climatic conditions which, in turn, can be related to the fire regime (Pausas & Keeley, 2014). In fact, adaptation to fire regimes and acclimation to harsher conditions (e.g., more frequent and intense droughts) in populations located near the limits of their environmental niche may promote greater resilience in these populations (Lloret & Kitzberger, 2018; Solarik *et al*., 2018).

To ecologically understand the response of population recruitment under diverse climatic conditions that occur before and after wildfires, and to evaluate the implications for the fate of these populations under climate change scenarios, the realized species' climatic niche offers a powerful study framework (Larson *et al*., 2023). The climatic niche can be inferred or estimated by translating the climatic characteristics of the sites where the species is present in the territory to an environmental space constructed with climatic variables. Despite the resulting simplification of species niche characteristics, this approach has proven to be robust enough to interpret the differential responses of co-occurring woody species (Batllori *et al*. 2020; Pérez Navarro *et al*., 2019; Pérez-Navarro *et al*. 2024; Sapes *et al*., 2017) or of populations of the same tree species across geographic gradients (Elvira *et al*., 2021; Lloret & Kitzberger, 2018; Margalef-Marrase *et al*., 2020). This approach is thus particularly useful to assess population resilience in the face of disturbances, such as wildfires and extreme climate events (e.g., heat waves and droughts), and the interactions among them.

1.4 PhD Thesis case study and objectives

During the last decades, high climatic variability together with changes in land management has resulted in a significant increase in the frequency and intensity of wildfires and drought events across many biomes, including Mediterranean forests. In Spain, wildfires have been responsible for the loss of 24% of the forest cover between 2001 and 2019 (Tyukavina *et al*., 2022). Additionally, in extreme years such as 1994 (Piñol *et al*., 1998) or 2003 (Garcia-Herrera *et al*., 2010) fire seasons, wildfires caused a large proportion of the total burned area in the Iberian Peninsula in the last decades. Fires have affected different Mediterranean forest types, causing losses in biomass and ecosystem alterations that can surpass the regeneration capacity of the populations (Karavani *et al*., 2018). Yet, improved scientific understanding on the role of different drivers (e.g., climate, regenerative traits, site properties) in explaining the observed vegetation responses after fire is needed, especially concerning compound fire-drought regimes. This is especially relevant under future scenarios of altered fire regimes and their interaction with increasing drought, which may jeopardize ecosystem resilience.

The general objective of this PhD Thesis is to study the effect of compound disturbance regimes (wildfires and droughts) on the resilience of Mediterranean forested ecosystems at different levels (from individuals to populations), incorporating the influence of species regenerative strategies (seeding, resprouting and fire-sensitive) and the climatic conditions. Specifically, I assessed how fire properties and climatic variability before and after fires influence post-fire tree regeneration at different regional scales: in the Eastern coast of the Iberian Peninsula (Catalonia and Valencia community) in sites that burned between 1994 and 2013 (Chapter 2), in Catalonia in sites that burned between 2002 and 2013 (Chapter 3), and across Spain in sites that burned between 1996 and 2007 (Chapter 4). The influence of pre- and post-fire climatic variability (indicative of drought conditions) was characterized through the species' realized climatic niche framework. The assessment of the variability in regeneration patterns of *Pinus halepensis*, *Quercus ilex* and *Pinus nigra* were used to infer resilience and dynamics of the vegetation after fire. The climatic niche framework allows assessing how populations' position in niche space (i.e., distance to the niche optimum or the edge of the climatic niche) could affect post-fire regeneration and thus ecosystem resilience.

The specific objectives of the different chapters that conform this PhD Thesis are:

In Chapter 2, the goal is to study the resilience of *Pinus halepensis* Mill. populations in burned areas in east Spain (Catalonia and Valencia community) that have experienced compound fire-drought regimes. For this purpose, I analyzed the post-fire regeneration of *P. halepensis* populations considering the climatic conditions associated with drought episodes in the years previous and following wildfires. Importantly, I characterized the climate position of burned populations in relation to the environmental space (realized climatic niche) defined by the climatic conditions where *P. halepensis* occurs across its Spanish distribution range. I sampled the density of *P. halepensis* recruits after fire over a gradient of pre- and post-fire drought conditions along the Eastern coast of the Iberian Peninsula. In each study site, I characterized pre- and post-fire climatic conditions (particularly those related to drought) and translated them into the species' climatic realized niche to compute deviations from the species' climatic niche optimum. I hypothesized that drought conditions after the fire may jeopardize the regeneration through limited seedling establishment, whereas drought conditions before the event may limit seed production. Finally, I expected that fire severity and its interaction with pre- and post-fire climate conditions would positively influence post-fire regeneration patterns by diminishing competition effects.

In Chapter 3, the aim is to identify how post-fire climatic conditions (position within the climatic niche) and microsite characteristics modulate the development of *P. halepensis* individuals after fire. With this purpose, I analyzed the performance in terms of plant size of *P. halepensis* recruits established after wildfires in nineteen burned areas of Catalonia (NE of Spain). I estimated the germination year of post-fire recruiting individuals through root collar sections and characterized their microsite environment considering soil rockiness and vegetation cover. The climatic conditions of the years following germination were characterized according to the species' climatic niche defined by *P. halepensis* occurrences across its European distribution range. The main hypothesis was that together with microsite characteristics, position in niche space after the wildfire (distance to niche optimum and niche edge of the recruiting populations) modulates recruits' performance. Specifically, I expected that the size of *P. halepensis* recruits, including height, basal area and crown size, would be lower when the climatic conditions after the wildfire have been closer to the drier edge of the species' climatic niche.

In Chapter 4, the goal is to assess the post-fire regeneration of three dominant tree species in the Mediterranean Basin with contrasted regenerative strategies, *P. halepensis* (seeder), *Quercus ilex* L. (resprouter) and *Pinus nigra* J.F.Arnold (fire-sensitive), in relation to populations' position in their respective climatic niche space. For this purpose, I characterized species resilience as the capacity to recover the canopy and the capacity to maintain itself as the dominant tree species of the tree community after the fire. I assessed the role of pre- and post-fire climatic conditions by characterizing the climate position of burned populations of the three species concerning their environmental spaces (realized climatic niche of each species), as defined by the climatic conditions of *P. halepensis, P. nigra* and *Q. ilex* occurrences across their European distribution range. The main hypothesis was that the position of the populations in niche space before and after the fire modulates post-fire resilience, and that irrespective of regenerative strategy, higher resilience occurs in locations closer to the niche optimum and far from the dry edge (i.e., characterized by drought-related conditions).

In Chapter 5, I aim to discuss how the results from my investigations can help us to propertly use the realized climatic niche as a tool toward a better understanding of the resilience of the Mediterranean tree species to compound fire-drought regimes. I also discuss the species' potential ability to front the future scenarios of climate change where disturbance regimes are supposed to change towards larger, more frequent and more intense fires coupled to increased drought conditions. Besides, I discuss how other variables such as fire severity or competitive processes can interact with climatic conditions to modify the response of the populations to compound disturbance regimes.

Chapter 2

Species' climatic niche explains post-fire regeneration of Aleppo pine (*Pinus halepensis* Mill.) under compounded effects of fire and drought in east Spain

Abstract

Fire and drought are two major agents that shape Mediterranean ecosystems, but their interacting effects on forest resilience have not been yet fully addressed. We used *Pinus halepensis* to investigate how compound fire-drought regimes determine the success of post-fire regeneration. We measured the density of *P. halepensis* newly established individuals following wildfire in forty-three sites along the Spanish east coast, the wettest region of the species distribution. The climatic niche of *P. halepensis* was characterized by considering their populations across its Spanish distribution range. We used yearly values (1979-2013 period) of accumulated precipitation, mean temperature and the warmest quarter values of these two variables to generate the climatic space (or climatic niche) occupied by the species. Kernel density estimates were then applied to determine the niche optimum, which would correspond to the species' climatic optimum within its Spanish distribution range. Then, we computed the pre- and post-fire climatic deviations of each sampling site as the difference between site-specific climate conditions respect to the species niche optimum and assessed their relationship with the success of post-fire regeneration. We found highly variable patterns of post-fire regeneration density of *P. halepensis* over the studied sites, ranging from 7 to 42822 tree pines ha^{-1}. Generalized linear models indicated a positive relationship between fire severity and the density of *P. halepensis* regeneration. Positive temperature deviations - warm conditions - before fire were positively related to pine regeneration. This effect increases under higher fire severity. By contrast, warm temperatures after fire showed a negative effect on the density of pine trees. Positive precipitation deviations - wet conditions - after fire enhanced pine regeneration, while precipitation before fire did not have any significant effect. Though *P. halepensis* is considered a species adapted to fire and drought, the interaction between these two disturbances can alter the success of its post-fire recovery patterns, thus limiting the species' resilience in the future.

2.1 Introduction

Compound disturbance regimes can have a deeper impact on ecosystems than the influence of disturbances acting separately (Batllori *et al.*, 2019; Buma, 2015). In forest ecosystems, the ability to cope with disturbances - resilience - largely relies on post-disturbance regeneration (Johnstone *et al.*, 2016; Martínez-Vilalta & Lloret, 2016). Of the many disturbances affecting forested ecosystems on Earth, drought and wildfires are among the ones with a strongest influence on vegetation patterns and dynamics (McDowell *et al.*, 2020). Drought occurs as a result of two climatic conditions, low precipitation values and high temperature, that promote elevated evapotranspiration rates. Importantly, it can jeopardize post-fire recovery by modulating the success of both recruits' establishment and regrowth of surviving organs (Davis *et al.*, 2019; Karavani *et al.*, 2018). The compound regime of drought and wildfires acquires particular relevance in a global change context, with an expected increase in temperature, and more frequent and intense episodes of heat and drought.

The effects of compound disturbance regimes in terrestrial ecosystems are investigated in many cases through modelling perspectives (e.g., Batllori *et al.*, 2017; Baudena *et al.*, 2020; Henzler *et al.*, 2018). However, increased empirical understanding of the influence of interacting disturbances on ecosystem resilience is needed to better anticipate the consequences of ongoing global change to vegetation patterns. For instance, high fire intensity can favour the recruitment of seeder species which release seeds stored into serotinous cones or fruits, or can activate seeds stored into the soil (Keeley, 1995). After fire, the newly established seedlings find environments with reduced competition and increased key resources (Marañón-Jiménez *et al.*, 2013; Moya *et al.*, 2007). However, successful recruitment, which eventually determines population resilience (Ibáñez *et al.*, 2019), is influenced by climate components associated with drought (Baudena *et al.*, 2020; Davis *et al.*, 2019), which may be temporally coupled with wildfires. Therefore, species regeneration ability after disturbance events such as wildfire, and the influence of pre- and post-fire extreme climate conditions (e.g., drought) on such regeneration patterns can largely determine the resilience capacity of populations.

Regenerating populations of any given species across the territory experience particular conditions in relation to the species' climatic requirements or species niche (Fréjaville *et al*., 2018; Grubb, 1977; Pironon *et al*., 2018; Rosbakh *et al*., 2018). The species' niche is shaped by the environmental characteristics of the sites where the species occurs, i.e., the realized climatic niche that also includes the influence of biotic interactions (Carscadden *et al*., 2020; Peterson, 2011). It can be hypothesized, following the Centre-Periphery Hypothesis (CPH), that climatic conditions close to species' limits of tolerance or niche edge may support low regeneration levels and, therefore, limited resilience to disturbance (Martínez-Meyer *et al*., 2013; Osorio-Olvera *et al*., 2019; Sexton *et al*., 2009). By contrast, populations that grow in locations with climatic conditions close to the ones that characterize the centroid or optimum of the species' niche can be assumed to have high resilience, due to better physiological conditions of their individuals (Lynch *et al*., 2014; Pérez Navarro *et al*., 2018). Systematic assessment of regeneration success after disturbance and, therefore, resilience in relation to population position within the niche space is still lacking.

Mediterranean Basin may be one of the most affected areas by changes in the compound regime of wildfire and drought under future climates, since higher temperatures and lower precipitation levels during summer are expected (IPCC, 2014; Ozturk *et al*., 2015; Spinoni *et al*., 2018). Also, agricultural abandonment is promoting fuel accumulation across the landscape (van der Zanden *et al*., 2017), increasing the risk and magnitude of fires (San-Miguel-Ayanz *et al*., 2013). In this study, we aim to investigate the effect of fire severity and drought conditions before and after the fire on the regeneration of *Pinus halepensis*, a key tree species in the Mediterranean Basin. This species is well adapted to wildfires (Espelta *et al*., 2011) and to the seasonal summer drought conditions that characterize the Mediterranean climate (Sheffer, 2012). However, under ongoing climate change, *P. halepensis* can experience increased mortality due to drought (Pérez-Navarro *et al*., 2020), particularly during the initial steps of establishment (Chambel *et al*., 2013). The foreseen increment of drought frequency and intensity could thus promote extreme drought conditions before or after fire, constraining regeneration and reducing the resilience of this species (Batllori *et al*., 2017, 2019; Baudena *et al*., 2020). Nevertheless, empirical evidence of how the compound regime of fire and drought (i.e., intense drought conditions before or after the fire) modulate post-fire regeneration success of this key species is still required.

Here, we analysed *P. halepensis* post-fire regeneration in relation to the climatic conditions associated with drought in the years previous and following wildfire. Importantly, we characterized the climate conditions of burned populations in relation to an environmental space defined by the climatic conditions where *P. halepensis* occurs across its Spanish distribution range. We sampled the density of *P. halepensis* recruits after fire over a gradient of pre- and post-fire drought conditions along the Eastern coast of the Iberian Peninsula. For each study site, we characterized pre- and post-fire climatic conditions (particularly those related to drought) and translated them into the species' climatic niche to compute deviations from the species' climatic optimum. We hypothesized that drought conditions after the fire may constrain the regeneration through limited seedling survival, whereas drought conditions before the event may limit seed production. Finally, we expected that fire severity and its interaction with pre- and post-fire climate conditions will positively influence post-fire regeneration patterns by diminishing competition effects.

2.2 Material and methods

Study species

Pinus halepensis Mill. (Aleppo pine) distribution ranges from the West (Spain, Morocco) to the East (Lebanon) of the Mediterranean Basin (Mauri *et al*., 2016a). This species is most abundant in thermo- and meso- Mediterranean areas, but it also inhabits mountain regions close to the coast, where it appears at lower altitudes. It is well adapted to the dry summer conditions characteristic of Mediterranean climate (Chambel *et al*., 2013), and its suitable climatic area over the Mediterranean Basin is expected to enlarge according to future climate change models (Urli *et al*., 2014).

This pine is a serotinous, post-fire seeder whose seed release is promoted by fire due to a massive heat-induced opening of the cones retained in the crown (Palmero-Iniesta *et al*., 2017; Tapias *et al*., 2004). This, together with its physiognomic characteristics (e.g., accumulation of lower branches and dead biomass), makes it a pyrophyte species that can regenerate quickly after fire. However, its successful regeneration requires moderate rains following the fire (De Luís *et al*., 2005; Mendel *et al*., 1997; Retana *et al*., 2002).

Additionally, the species attains sexual maturity in 12-20 years (Macias *et al*., 2006), requiring on average 15 years after the fire to accumulate a canopy seed bank abundant enough to recover after fires.

Study area and sampling design

Field sampling was carried out in burned areas across the *P. halepensis* distribution in the Eastern coast of the Iberian Peninsula (Figure 2.1). Forty-three areas that burned between 1994 and 2013 were sampled (Supplementary Material, Table SM2.1). We selected fires that burned only once since 1994 to avoid the effects of high-fire recurrence on seed bank availability (Eugenio *et al*., 2006; Eugenio & Lloret, 2006; Santana *et al*., 2014). To capture the influence of pre- and post-fire climatic conditions, we used the standardized precipitation evapotranspiration index SPEI (Vicente-Serrano *et al*., 2010) to perform a balanced selection of sampling sites. The sampling design included (i) 14 sites with drought occurring before the fire, corresponding to areas with SPEI values lower than -0.8 during the three years before the fire and with at least a severe drought episode (SPEI lower than -1.5) included within this period, (ii) 14 sites with drought occurring after the fire, corresponding to areas with SPEI values lower than -0.8 during a year and a half after the fire, and (iii) 15 sites without drought before or after fire, corresponding to those areas where SPEI values were positive during both periods. The sampling sites had a wide range of *P. halepensis* basal area measured previous to the fire (estimated from the closest Spanish National Forest Inventory plots, IFN1 and IFN2, to the sampled areas, Villaescusa & Díaz, 1998). The lack of a significant relationship between basal area in these IFN sites and our estimations of post-fire pine density (IFN1 and IFN2 with p value= 0.146 and 0.186, respectively), reinforce the analysis of other factors such as climate and fire severity in determining post-fire regeneration success.

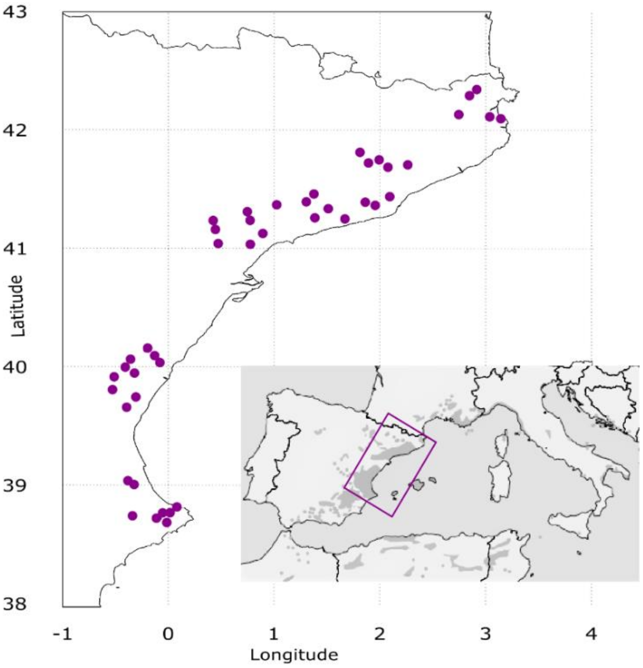


Figure 2.1: Site location (N = 43) along the east coast of the Iberian Peninsula where *Pinus halepensis* regeneration after fire was assessed. The inset map shows the location of the region within the species distribution area in the western Mediterranean Basin (modified from Fady *et al*., 2003). The UTM of each location can be consulted in the Supplementary Material, Table SM2.1.

Field surveys to assess post-fire regeneration were carried on in summer-fall 2019. In each site, we randomly selected a number of sampling points (replicates) proportional to the burned area, with approximately one point per hectare (mean: 14, range: 5-20 points per fire, N = 602 points in total). In order to assess the influence of pre- and post-fire climate on post-fire regeneration patterns, we focus on the success of post-fire regeneration from seeds produced within the burned population. Therefore, sampling points were located at a minimum distance of 100 m from the edge of the unburned forest or any isolated surviving tree to avoid the contribution of seeds subsequently arriving after fire from surviving trees (Broncano *et al*., 2005). Additionally, sampling was mostly focused in drier, south-facing slopes to emphasize the effect of drought conditions and to better capture fire-drought interactions.

We used the Point-Centered Quarter method (PCQ, Bryant *et al*., 2005; Cottam & Curtis, 1956) to estimate the regeneration density (individuals ha^{-1}) of pines after the fire in each sampling point. In each sampling point we established four 90° quarters and measured the distance from the central point to the closest regenerating pine in each quarter. The density of pine regeneration was then calculated following the formula $DH = \sum_{i=4}^{i=1} dQ_i^{-2}/4 \times 10^4$, where DH is regeneration density per hectare and dQ_i (i from 1 to 4) is the distance in meters to the closest pine in each quarter. Finally, we obtained the mean pine regeneration density per hectare in each of the 43 assessed fires by averaging the values of regeneration density of the replicate points performed in each fire. In those quarters where no pines were found within a distance of 70 m, regeneration density was considered to be null. Given that we sampled burned areas encompassing different time lags after the fire (from 6 to 25 years after fire), we standardized the obtained density estimates DH to avoid underestimating regeneration in older fires due to mortality of young plants. Specifically, density estimates were adjusted using the survivorship function $Survival\, density = DH \times 104.5\ (years\ after\ the\ fire\ event)^{-0.274}$ defined by Broncano *et al*. (2005).

<u>Climatic niche characterization</u>

We characterized *P. halepensis*' climatic niche in its western distribution range (i.e., Iberian Peninsula without Portugal) using two sets of yearly climatic data obtained from CHELSA (Karger *et al*., 2017, period 1979-2013): (1) total precipitation and mean annual temperature and (2) total precipitation and mean temperature of the warmest quarter. We used the temperature and precipitation of the warmest quarter since summer is the driest season in Mediterranean climate, which may limit the survival of recently emerged pine seedlings (Lloret *et al*., 2004; Seidel & Menzel, 2016)

First, we extracted the above-mentioned climate variables from all geographic locations in which the species was recorded in the Spanish National Forest Inventory, IFN3 (Bombín & Cezón, 2018). We included 8982 plots where *P. halepensis* was recorded as the dominant species; the plots where separated at least 1km from each other (Bombín & Cezón, 2018) . We extracted yearly climate values for 1979-2013 period instead of the average values of the whole period to better characterize the inter-annual variability in environmental conditions experienced by the species (Perez-Navarro *et al* 2020). Second, we built two environmental spaces: one defined by annual values of temperature and precipitation, and other defined by the values of these variables during the warmest quarter. Then, the density of species occurrence within these climatic spaces was computed through kernel density estimates (i.e., the realized climatic niche; Broennimann *et al*., 2012). The species climatic optimum was computed as the centre of mass of *P. halepensis* density occurrence in the climatic space, that is, the point with the highest species density within the climatic niche. The coordinates of the optimum of the niche built with mean, annual variables correspond to 14.4 C° of temperature and 427.0 mm of precipitation, while the optimum of the niche constructed with the warmest quarter variables corresponds to 23.0 C° of temperature and 12.3 mm of precipitation, reflecting the dry season in Mediterranean climate (Figure 2.2).

Site-specific climatic deviations in niche space

We translated the temperature and precipitation values, both annual and warmest quarter variables, for each of the 5 years before and after the wildfire event for each sampling site within the computed climatic niches. Then, we calculated the yearly climate deviations of temperature and precipitation (Table 2.1) within this 10-years window around fire as the distances between the specific conditions of each study site and the species niche optimum (i.e., the distance to niche optimum in the two axes of the space defined by temperature and precipitation, Figure 2.2). The time before or after the fire (5-years window in each case) was included to weigh for delayed effects of climate deviations in relation to the density of regeneration. Deviation of each year was weighed using the formula $WD = CD * \text{time before or after fire}^{-1}$ (WD= weighed deviation, CD= climate deviation). We used the weighted average distances of these pre- and post-fire periods to determine the deviations in temperature and precipitation before and after fire. These deviations represent the degree to which each burned site was subjected to drier/wetter or warmer/colder conditions concerning the species niche optimum before and after the wildfire event. In four sites that burned in 2009, 2012 and 2013, data over the entire 5 years' window after the fire were not available (CHELSA annual climate database covers the period 1979-2013); for these sites, the analysis only considered 4, 1 and 0 years after the fire, respectively.

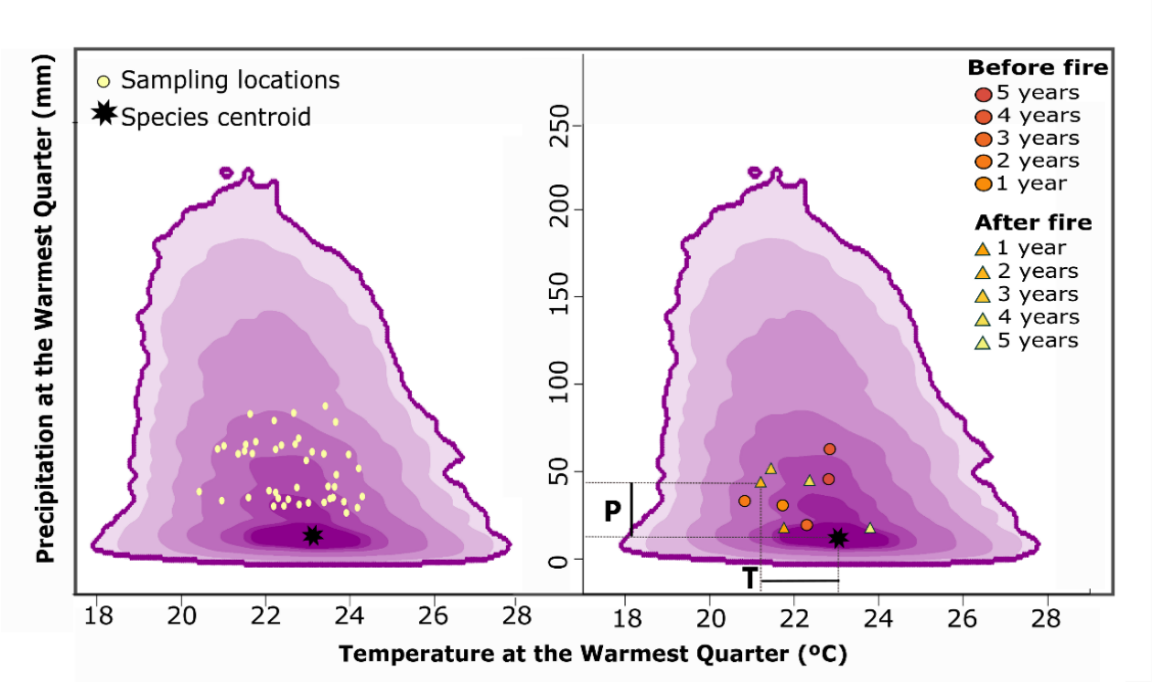


Figure 2.2: *Pinus halepensis*' climatic niche characterized with yearly values of temperature and precipitation of the warmest quarter (period 1979-2013) in sites where the species inhabits in Spain. The black star depicts the niche optimum which would correspond to an estimation of the species' climatic optimum. On the left, the location of the historical (1979-2013) average conditions of each of the forty-three sampled fires (yellow dots) within the climatic niche is depicted. On the right, an example of the 5 years pre- and post-fire conditions for one of the sampled fires is shown to illustrate how we assessed pre- and post-fire temperature (T) and precipitation (P) deviations in niche space in relation to the species' climatic optimum in each study site.

Fire severity characterization

We used the delta normalized burn ratio (dNBR) to assess fire severity in each sampling site. First, we computed fire severity within the area burned in each study site from Google Earth Engine® following Parks *et al.*, 2018 (https://code.earthengine.google.com/c76157be827be2f24570df50cca427e9 last entry 20/03/20). The dNBR was produced using Landsat TM, ETM+ and OLI imagery that registers NIR (near infrared band) and SWIR (shortwave infrared band). Then, we extracted the dNBR value for each sampling point within each fire and computed a mean severity value representative of each study site.

Statistical analysis

Generalized linear models (GLM) with normal distributions were used to assess the relationship between the density of post-fire pine regeneration in each site and pre- and post-fire climatic deviations and fire severity (dNBR). All predictor variables were standardized by subtracting their mean value and diving by their standard deviation. Two sets of models (Supplementary Material, SM2.2 and SM2.3), without and with variable interactions, were performed using the temperature and precipitation deviations within the climatic niche built from annual mean and warmest quarter climatic variables. Final models were selected according to the stepwise selection procedure based on the Akaike information criterion (AIC) using the *dredge* function of MuMIn package (Bartoń, 2019).

All statistical analyses were performed in R version 3.6.3 (Team R D. C., 2018).

2.3 Results

The density of *P. halepensis* regeneration after fire fluctuated between 7 and 42822 recruits ha^{-1}, with a mean value of 4324 recruits ha^{-1} (sd = 9370), encompassing thus a wide gradient of post-fire regeneration success within the sampling sites (Supplementary Material, Table SM2.1).

The deviation of temperature and precipitation of the assessed populations with respect to the species climatic optimum showed a wide range in both pre- and post-fire conditions and for both annual- and warmest quarter-based climatic niches (Table 2.1). Precipitation exhibited the highest deviation values when considering the annual-based niche computations. Positive deviation values of temperature and precipitation correspond to warmer and wetter conditions, respectively.

Table 2.1: Variability in deviations of temperature and precipitation in the studied *Pinus halepensis* populations in relation to the annual- and warmest quarter-based niche of the species within its Spanish distribution range. The table shows the standardized, minimum, mean, maximum and standard deviation values of the climatic deviation to the respective niche optimum; raw deviation values are provided into brackets.

		WARMEST QUARTER-BASED NICHE				ANNUAL MEAN-BASED NICHE			
		MIN	MEAN	MAX	SD	MIN	MEAN	MAX	SD
TEMPERATURE DEVIATION (°C)	BEFORE FIRE	-0.058	-0.007	0.042	0.024	-0.025	0.040	0.131	0.042
		(-1.333)	(-0.162)	(-0.954)	(-0.555)	(-0.414)	(-0.579)	(-1.885)	(-0.606)
	AFTER FIRE	-0.055	-0.005	0.054	0.024	-0.021	0.050	0.203	0.046
		(-1.270)	(-0.118)	(-1.230)	(-0.552)	(-0.272)	(-0.721)	(-2.926)	(-0.666)
PRECIPITATION DEVIATION (MM)	BEFORE FIRE	0.069	1.364	1.863	0.751	-0.051	0.203	0.535	0.142
		(-1.593)	(-16.779)	(-42.846)	(-9.240)	(-21.932)	(-86.737)	(-227.665)	(-60.730)
	AFTER FIRE	0.061	1.277	1.945	0.908	- 0.040	0.190	0.641	0.160
		(-1.393)	(-15.705)	(-44.743)	(-11.171)	(-17.209)	(-80.965)	(-273.888)	(-68.272)

Considering the annual mean-based niche, the GLM without interactions revealed a significant, positive relationship only between density of regeneration and fire severity (dNBR) (p-value < 0.01; Figure 2.3; Supplementary Material, Table SM2.2). The most parsimonious model considering interactions included precipitation before fire, severity and their interaction (Figure 2.3). Fire severity and its interaction with the deviation of precipitation before fire showed a significant, positive effect in the density of regeneration (p-value < 0.01 and <0.05 respectively, Supplementary Material, Table SM2.3).

When considering the warmest quarter-based niche, the final model without interactions showed a significant, positive effect of fire severity (dNBR) on the density of regeneration (p-value < 0.01; Figure 2.3; Supplementary Material, Table SM2.2). Similarly, deviations in the climate space of pre-fire temperature (warmer conditions) and post-fire precipitation (wetter conditions) also showed a positive, significant relationship with pine regeneration (both p-value < 0.05; Supplementary Material, Table SM2.2). By contrast, post-fire temperature deviations showed a negative, significant relationship with the regeneration density (p-value < 0.05; Supplementary Material, Table SM2.2). The most parsimonious model considering interactions between predictor variables was the one including pre- and post-fire temperature deviations, fire severity (dNBR), and their interaction (Figure 2.3; Supplementary Material, Table SM2.3). Fire severity and its interaction with the deviation of temperature before fire had a significant, positive effect in the density of regeneration (both p-value < 0.01), whereas the interaction of fire severity with the temperature deviation after the fire showed a negative effect in regeneration (p-value < 0.01). Specifically, high fire severity is related with high regeneration density when it interacts with positive pre-fire temperature deviations (i.e., warmer conditions; Figure 2.4A) or with negative post-fire temperature deviations (i.e., cooler conditions, Figure 2.4B).

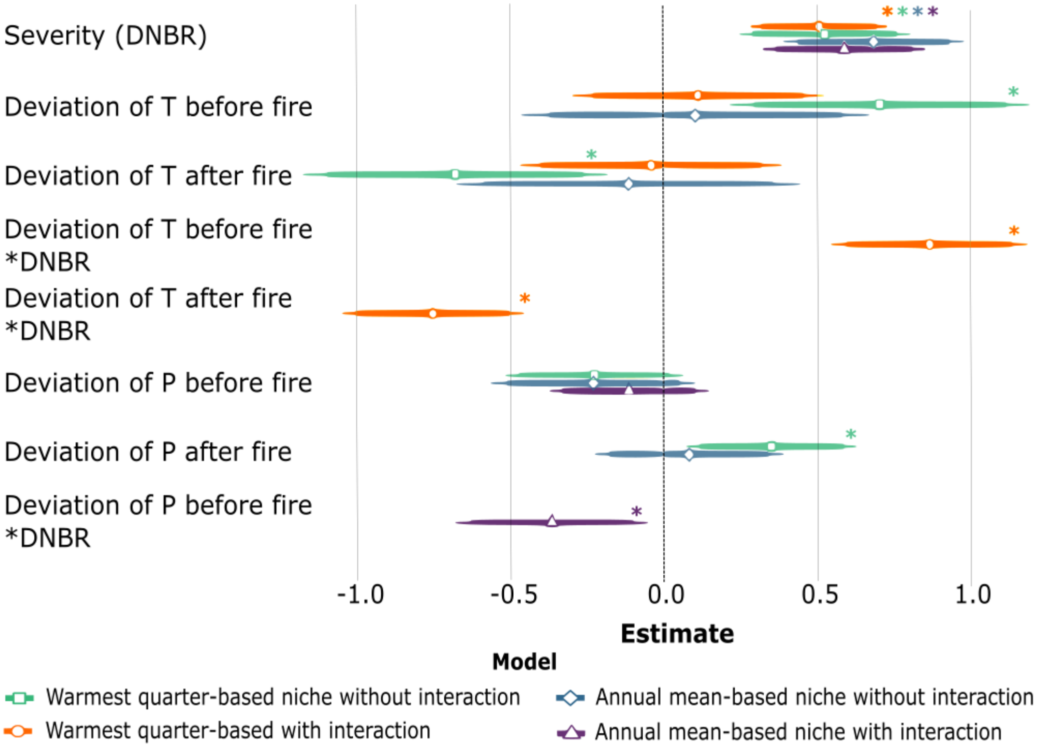


Figure 2.3. Models coefficient estimates from the models built with climatic variables of the warmest quarter-based niche (WQ) and with the variables of the annual mean-based niche (AM) to assess the relationship between *Pinus halepensis* regeneration and environmental deviations in temperature (T in the figure) and precipitation (P in the figure) before and after the fire (±5-years window for each period; see Figure 2) and fire severity in each study site. Results of the models of WQ without (green) and with (orange) interactions and AM with (purple) and without (blue) are shown. The models with interactions only included the variables selected by stepwise analyses. The asterisks indicate the variables with a significant effect on the density of pine regeneration (p< 0.05) in each model. All cases in which coefficient estimates are in contact with the vertical discontinuous line correspond to non-significant variables in the model. The thicker section represents the 90% confidence interval.

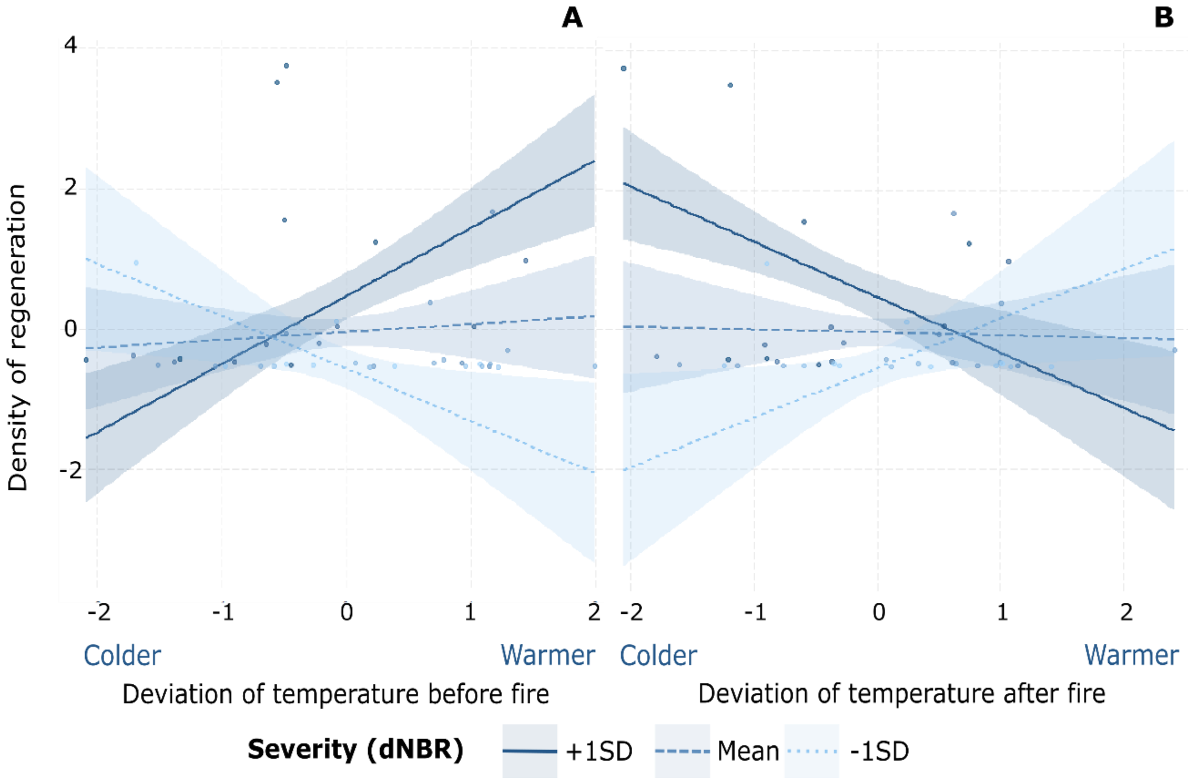


Figure 2.4. Effect of the interaction between fire severity (dNBR) and temperature deviations 5 years before (A) and after (B) the fire in the regeneration density of *Pinus halepensis* corresponding to the model considering the niche space built with climatic variables of the warmest quarter. Note that under high fire severity (thick dark blue line), density of regeneration increases with positive temperature deviations before fire (warmer conditions, A plot), and also with negative temperature deviations after the fire (B plot). Whereas under low fire severity (dotted light blue line), the relationships show the opposite trends.

2.4 Discussion

This study shows how the interacting effect of the components of the fire-drought compound regime, severity of the wildfire event and the variability of climatic conditions, modulate regeneration success of a key tree species of the Mediterranean Basin. In the current study, the density values of the pine recruits after fire exhibited wide variability, but the mean measured value (4324 recruits ha^{-1}) was lower than the values reported in the European literature (Capitanio & Carcaillet, 2008; Daskalakou & Thanos, 2004; Fournier *et al*., 2013). We found that the success of *P. halepensis* post-fire regeneration is determined by both pre- and post-fire climatic deviations of the burned populations relative to the species niche optimum in climatic space. Importantly, the interaction with the severity of fire modulates the influence of such climatic deviations, showing the relevance of the compound fire-drought regime. Additionally, climatic deviations in relation to species optimum have different effects on post-fire regeneration when they occur before or after the wildfire event, highlighting the importance of the sequence of events to ecosystem resilience (Batllori *et al*., 2019).

Pinus halepensis populations that experienced high post-fire precipitation during the warmest quarter, compared to the species niche optimum, showed high post-fire pine regeneration. This emphasizes the importance of the relatively wet conditions to successful seedling establishment (Baudena *et al*., 2020; Parra & Moreno, 2018; Pausas & Keeley, 2014), even for a seeder species such as *P. halepensis* that can regenerate under xeric conditions (Arnan *et al*., 2007). By contrast, pre-fire precipitation deviations in the warmest quarter did not appear significantly related to regeneration success in our study sites. Either seed bank accumulation is not directly related to precipitation at the temporal scale considered here (i.e., 5 years window before fire), or the sampled populations were located close enough to the wetter edge of *P. halepensis*' climatic niche in the study area (Figure 2.2), limiting the capacity of discrimination of this variable in our assessment.

Positive temperature deviations before the fire event were positively related to the post-fire density of pine regeneration. The study sites, as stated above, were located in the wetter range of the climatic niche obtained from populations over the entire Iberian Peninsula (Figure 2.2, Table 2.1). Thus, higher temperatures before fire in the sampled sites would have enhanced tree growth and seed production although positive temperature deviations (i.e., warmer conditions in relation to the species climatic optimum) after fire were negatively related to post-fire regeneration density. This could be reflecting the high sensitivity of newly established plants, with a still poorly-developed root system, to high temperatures, reinforcing the effects of the typically dry conditions of Mediterranean ecosystems on seedling survival (Baudena *et al*., 2020; Galiano *et al*., 2013; Pausas & Keeley, 2014; Pratt *et al*., 2014). Overall, our findings highlight the importance of both pre- and post-fire climatic conditions to the mechanisms building forest resilience. These conditions may have contrasting effects according to the processes that they determine, seed production before fire or seedling survival after it, regarding to the potential differences between adult and regeneration niches (*sensu* Grubb 1977).

We found that the post-fire regeneration of *P. halepensis* was enhanced by fire severity, in agreement with previous studies reporting reduced regeneration of this species with low-severity fires, (Fournier *et al*., 2013). *Pinus halepensis* is a heliophilous species that needs open conditions to regenerate successfully. The loss of vegetation cover during high-severity fires may increase the availability of open spaces in the post-fire community, thus promoting the regeneration success of this species. Also, seed release from its serotinous cones can be enhanced by high temperatures attained during the wildfire (Palmero-Iniesta *et al*., 2017). However, extremely dry weather before the fire may have triggered cone opening. This, together different degrees of serotiny, may have influenced the effective post-fire seed dispersal across the studied populations (Hernández-Serrano *et al*., 2013; Ne'eman *et al*., 2004). We could not assess the influence of these factors on the observed regeneration patterns since there is not comprehensive information of climate-induced cone opening or serotiny variability for the species within the studied populations and across its geographical range. Nevertheless, the relationship between fire severity and regeneration may not be linear and it may decrease at very high levels of fire temperature (Viana-Soto *et al*., 2017). The significant, opposite effects of the interaction of fire severity with deviations in temperature before and after fire (Figure 2.4) further reinforce this non-linear relationship between fire severity, climate and regeneration success. Also, this provides empirical evidence of the reported, model-inferred importance of fire-drought interactions to successful forest recovery in Mediterranean environments (Batllori *et al*., 2019; Baudena *et al*., 2020).

The combination of warmer conditions before fire with high fire severity favoured pine regeneration density in the studied populations sited in the Eastern coast of the Iberian Peninsula. This could be reflecting the increment of seed production during pre-fire years (Richardson *et al*., 2005; Schauber *et al*., 2002), particularly in those localities located at the wetter range of the species' distribution (in Iberian Peninsula without Portugal), coupled to the removal of other competitive species under high severity fires. Low severity fires are associated with higher post-fire competition with other species (Fournier *et al.*, 2013), thus diminishing the success of the regenerating pine seedlings. By contrast, positive temperature deviations after the wildfire event have a negative effect on the density of pine trees when they interact with high fire severity. This could reflect the high seedling sensitivity to dry conditions coupled with soil degradation (destruction of soil organic material, modification of the structure and water repellency increment) by high-severity fires (Zavala *et al.*, 2014).

We found that models based on climate variables of the warmest quarter explained pine regeneration better than models based on annual variables. This may illustrate the sensitivity of early demographic stages to extreme conditions, even when occurring over a short period of time, likely because they cannot store reserves that provide the capacity to buffer harsh environmental conditions (Chuste *et al.*, 2020). Additionally, in Mediterranean ecosystems harsh conditions arise seasonally in summer, the warmest and driest quarter, when high mortality rates of recently established plants can occur (Henzler *et al.*, 2018; Lloret & Zedler, 1991). The seasonal variables can better represent the temporal constraints on some phenological process of the plants that can be underrated using annual variables (Diez *et al.*, 2014). Therefore, our study shows the relevance of selecting the ecologically-meaningful climatic variables when assessing the sensitivity of those processes that determine forest resilience. In our case, temperature deviations in relation to species climatic optimum during the warmest quarter appears as a more relevant predictor than annual variables to assess the performance of the regenerating populations of *P. halepensis*, and merits consideration when assessing resilience in Mediterranean forests into the future.

We were able to explain post-fire regeneration of *P. halepensis* by characterizing climatic conditions in relation to the environmental space (climatic niche) in which this species is found, as a surrogate measure of drought conditions. In doing so, the variation of physical parameters such as temperature and precipitation is translated into biological responses, in terms of species abundance, which avoids the construction of complex models (e.g., species distribution models). The species' climatic niche, its abundance over climatic gradients, also incorporates the historical adaptation of the species to local conditions (Jump *et al.*, 2006), and it is likely to reflect species performance in the areas of geographical occurrence (Pironon *et al.*, 2018). Despite the well-known limitations of using species distribution data to characterize species' realized niche (Franklin *et al.*, 2013; Pearson *et al.*, 2006; Pearson & Dawson, 2003), this approach is robust enough to interpret differential responses of co-occurring woody species (Pérez Navarro *et al.*, 2018; Sapes *et al.*, 2017) or populations of the same tree species across geographical gradients (Lloret & Kitzberger, 2018; Margalef-Marrase *et al.*, 2020) in front of extreme drought episodes. Our results highlight the usefulness of the realized, climatic niche characterization to explain populations' demographic processes after disturbances and, specifically, their resilience under compound disturbance regimes (i.e., wildfires and droughts).

Although *P. halepensis* is well adapted to fire occurrence and drought conditions (Chambel *et al*., 2013; Mauri *et al*., 2016a) we found that certain combinations or sequences of these disturbances, such as negative post-fire deviations in precipitation (drier conditions) or positive post-fire deviations in temperature (warmer conditions) relative to the species optimum can jeopardize post-fire recruitment. This is further emphasized by the contrasted influence of the interaction between fire severity and pre- and post-fire temperature deviations. Future climatic scenarios predict the intensification of droughts and an increase of the frequency of heatwaves in Mediterranean areas (Ozturk *et al*., 2015) with important consequences on large wildfires (Ruffault *et al*., 2020). Our findings strongly suggest that these conditions are likely to affect negatively the regeneration capacity of *P. halepensis* forest after fire in this region as a result of fire-drought interactions. This would be due to potential synergistic effects of increased climatic fire risk and fire recurrence (Turco *et al*., 2018) with drought conditions on seed bank accumulation (e.g., sexual maturity age, Fernández-García *et al*., 2019) and seedling survival (Chambel *et al*., 2013). Overall, our study provides empirical evidence of the importance of the effects of compound disturbance regimes, such as fire and drought conditions, to ecosystem resilience even in species apparently well suited to the influence of these environmental agents acting separately. We also show that the species' climatic niche characterization, by assessing populations' climatic conditions relative to species climatic optimum, is a robust framework to analyze demographic responses and forest resilience under compound disturbance regimes.

2.5 Conclusions

Deviations in temperature and precipitation from the optimum of the realized species' climatic niche previous and posterior to the wildfire determine the post-fire regeneration density in *Pinus halepensis* populations in the Eastern coast of Spain. Warmer conditions before fire enhance pine recruitment probably due to the increase in seed production, but the opposite occurs if warmer conditions occur after wildfire, which will likely affect the seedlings' survivorship. The presence of wetter years after wildfires also promotes the high density of regeneration, because seedlings are sensitive to changes in resource availability, particularly to water in Mediterranean-type ecosystems. High-severity fires are related to higher densities of regeneration but the interaction with the climatic conditions can modify this relationship. The influence of climate conditions associated with drought episodes is better assessed when the realized species' climatic niche is used. The models used are more explicative when the extreme climatic conditions are considered using the warmest period (i.e. summer), rather than considering the annual variables.

Supplementary material

Table SM2.1. Sampling site location, year of fire and average post-fire density of regeneration (pines*ha^{-1}) and the management (MAN.) in each of them. Field sampling was carried out in burned areas (see FORESCAST; CGL2014-59742-C2-R2, Alvarez et al., 2024) along the *Pinus halepensis* distribution in the Eastern coast of the Iberian Peninsula (Figure 2.1). The post-fire management was recorder *in situ*, and we evaluated the grade of intervention considering if stumps or mechanically cut timber were found in one of the measured points (*), or if those were found in more than one point (**)

		ID	YEAR	LOCALITY	UTM			DENSITY	MAN.
CATALONIA	BARCELONA	19148	1994	ORDAL	31T	404349	4582923	172.14	
		19218	2013	VALLIRANA	31T	412193	4580128	2897.92	
		19220	1994	FIGARO I MONTMANY	31T	438364	4618702	1278.13	*
		19248	2001	VILLADORDIS	31T	407294	4619793	86.14	
		19251	2003	SANT LLORENÇ SAVALL	31T	422477	4616549	579.1	**
		19340	1994	LES PLANES	31T	423465	4587797	198.67	*
		19396	2006	SERRA GLOBUS	31T	400819	4629871	573.8	
		19512	2012	PANT. DE FOIX	31T	387941	4567971	1686.78	*
		19554	2003	TALAMANCA	31T	415341	4622714	439.47	**
	GIRONA	19286	2001	BANYOLES	31T	478452	4664416	17772.69	
		19486	2005	VILARIG	31T	487051	4682408	6045.77	*
		19546	2004	BIURE	31T	492542	4687923	16.71	
		19549	2001	L'ESCALA	31T	512189	4660749	5922.27	
		19568	2006	GARRIGOLES	31T	503500	4662039	22373.91	*
	TARRAGONA	19115	2009	MONTFERRI	31T	364262	4568975	349.98	
		19181	2005	BELLAGUARDA	31T	310876	4575914	3924.3	
		19201	1994	GANDESA	31T	287043	4547115	34.02	
		19241	1998	PONTILS	31T	363718	4592548	809.12	*
		19284	1997	JUNCOSA DE MONTMELL	31T	375013	4577287	269.99	
		19297	2002	TIVISSA	31T	312480	4545260	4929.01	
		19386	2007	PARC EOLIC	31T	322462	4555577	2284.53	*
		19407	2005	RIBA-ROJA D'EBRE	31T	284489	4567667	5298.59	
		19523	2000	CABRA DEL CAMP	31T	357601	4584458	156.06	
		19534	2006	RIUDABELLA	31T	334164	4581879	42822.26	*
		19579	1994	LA FATARELLA	31T	285362	4562107	1893.67	
		19668	2012	CABACES	31T	312679	4567974	35069.26	**

VALENCIAN COMMUNITY	VALENCIA	33934	2000	BARXETA	30S	726394	4326413	47.72	
		35797	1994	ALFARA DE BAIONA	30S	730424	4404372	488.22	**
		38822	2004	NÁQUERA	30S	722988	4394644	393.61	**
		39168	2005	SIMAT DE LA VALLDIGNA	30S	729452	4324546	495.2	
		41638	1994	ALTURA	30S	711336	4410728	125.19	*
	ALICANTE	34975	2000	ORBA	30S	756212	4296250	107.18	*
		36833	1999	BENIMAQUIA	31S	245996	4301077	7.08	
		37295	2000	ALDEA DE LAS CUEVAS	31S	239882	4297021	52.43	
		38007	2002	COLL DE RATES	30S	752451	4292593	286.9	*
		38384	2003	ERMITA DE LOS PINOS	30S	760014	4290265	244.62	*
	CASTELLÓN	34063	1994	LUDIENTE	30T	724712	4439254	232.99	
		35758	1994	FUENTES DE AYODAR	30T	720554	4432089	20632.74	*
		35777	1994	SAN JOAN DEL MORO	30T	744989	4443504	41.77	
		35788	1994	BORRIOL	30T	748596	4437001	131	
		36646	1999	SUERAS	30S	728217	4426713	4710.58	
		37519	2000	NOVALICHES	30S	712195	4422594	41.54	
		40181	2007	USERAS	30T	737680	4449322	29.18	

Table SM2.2. Results of the General Linear Model (GLM) without interaction between the deviation of the warmest quarter and severity compared with the model using annual mean variables.

	WARMEST QUARTER (P-R² = 0.57; AIC = 101.05)				ANNUAL MEAN (P-R² = 0.42; *AIC = 111.91)*			
	EST	SD	t val	P	EST	SD	t val	P
TEMPERATURE BEFORE FIRE	0.70	0.25	2.83	**0.01**	0.10	0.29	0.36	0.72
TEMPERATURE AFTER FIRE	-0.68	0.25	-2.68	**0.01**	-0.11	0.29	-0.40	0.69
PRECIPITATION BEFORE FIRE	-0.22	0.15	-1.52	0.14	-0.23	0.17	-1.34	0.19
PRECIPITATION AFTER FIRE	0.35	0.14	2.48	**0.02**	0.08	0.16	0.53	0.60
DNBR (SEVERITY)	0.53	0.14	3.69	**0.00**	0.69	0.15	4.57	**0.00**

Table SM2.3. Results of the full General Linear Model (GLM) with all interactions between the deviation of the warmest quarter and severity compared with the model using annual mean variables.

	WARMEST QUARTER (P-R² = 0.81; AIC = 92.51)				ANNUAL MEAN (P-R² = 0.60; *AIC =110.56)*			
	EST	ES	t val	P	EST	ES	t val	P
TEMPERATURE BEFORE FIRE	-0.00	0.40	-0.01	0.99	0.19	0.34	0.55	0.59
TEMPERATURE AFTER FIRE	0.07	0.46	0.15	0.88	-0.10	0.36	-0.29	0.77
PRECIPITATION BEFORE FIRE	-0.01	0.19	-0.07	0.95	-0.23	0.19	-1.18	0.25
PRECIPITATION AFTER FIRE	0.01	0.22	0.06	0.95	0.18	0.19	0.96	0.34
DNBR (SEVERITY)	0.49	0.15	3.36	**0.00**	0.63	0.18	3.49	**0.00**
TEMP * PREC BEFORE FIRE	0.34	0.36	0.95	0.35	0.42	0.19	2.16	**0.04**
TEMP * PREC AFTER FIRE	-0.12	0.38	-0.31	0.76	-0.35	0.23	-1.49	0.15
TEMP BEFORE FIRE *DNBR	0.86	0.24	3.66	**0.00**	0.19	0.34	0.55	0.59
TEMP AFTER FIRE *DNBR	-0.93	0.25	-3.66	**0.00**	-0.10	0.36	-0.29	0.77
PREC BEFORE FIRE * DNBR	0.38	0.24	1.55	0.13	-0.23	0.19	-1.18	0.25
PREC AFTER FIRE * DNBR	-0.23	0.21	-1.09	0.29	0.18	0.19	0.96	0.34

Chapter 3

Position in the climatic niche modulates post-fire performance of *Pinus halepensis* regeneration

Abstract

Fire is a primary driver in Mediterranean ecosystems, being post-fire regeneration a key process for their resilience. The bioclimatic factors that modulate regeneration success are, however, not fully known. We use *Pinus halepensis* as a model organism to investigate how local climatic conditions relative to the species' climatic niche, together with microsite conditions (neighbouring vegetation, soil stoniness) influence the performance of post-fire establishment. We characterized *P. halepensis*' climatic niche from its records in the EU Forest Inventory, crossing geographic occurrences with the respective yearly values of 12 bioclimatic variables for the period 1979-2018. Kernel density estimates were then applied to determine the climatic niche edge and the optimum (niche margin and centroid, respectively) within the environmental space defined by the PCA axis built from the bioclimatic variables. We also interpreted the bioclimatic variables in the PCA to compute the dry edge. We sampled, measured and aged newly established individuals in nineteen sites across Catalonia that burned once between 2002-2013. Then, we modelled plant height, basal area, crown diameter and green canopy in relation to the distance to the species niche optimum and dry edge during the period since plant establishment. As expected, height, crown diameter and basal area were positively correlated with age. Plant height was higher in plants located more distant from the dry edge of the climatic niche. However, pulses of years with climatic conditions closer to the dry edge, appeared positively correlated with recruits' height, likely due to population thinning under such drought conditions. Microsite characteristics modulated plant performance, being stoniness negatively correlated to recruits height, and surrounding *P. halepensis* cover promoting taller and narrower plants with less green canopy. The study reveals that position within the climatic niche offers a suitable framework to understand, together with microsite conditions, recruits' performance and thus post-fire regeneration patterns in a fire-resilient species such as *P. halepensis*.

3.1 Introduction

Fire shapes forested ecosystems worldwide, modifying their composition, structure and dynamics (McDowell *et al*., 2020; Whelan, 1995). These impacts on forests are largely determined by the components of the fire regime, including the spatiotemporal distribution, magnitude, frequency, seasonality and severity of fires (e.g., Keeley, 2009; Moreira *et al*., 2011; Viana-Soto *et al*., 2017). Climate change is imposing important modifications of fire regimes, due to more frequent and intense episodes of heat waves and drought, embebded in a trend of higher temperature, in many ecosystems (Grau-Andrés *et al*., 2024) and especially in the Mediterranean Basin (IPCC, 2023; Ozturk *et al*., 2015; Spinoni *et al*., 2018; Turco *et al*., 2018). The ultimate effects of these disturbances will be largely determined by vegetation's capacity to recover after wildfires, (i.e., its resilience, Johnstone *et al*., 2016), which in turn depends on several factors, such as climatic conditions, soils, biotic interactions and management (Baudena *et al*., 2020; McLauchlan *et al*., 2020). Importantly, the interaction between fire and other disturbances such as drought might impact ecosystems even more than the disturbances acting separately (Batllori *et al*., 2019; Baudena *et al*., 2020; Buma, 2015).

In Mediterranean-type ecosystems, vegetation succession after wildfire is largely characterized by a self-replacement of the species that dominated the community before the disturbance, a process also named auto-succession (Hanes, 1971; Pausas *et al*., 2004a; Xofis *et al*., 2021). Forest resilience to wildfires is basically dependent on regeneration, which is based on the mechanisms of the species to restore their populations from the establishment of recruits or the regrowth of surviving organs (i.e. stems, stumps, roots) (Davis *et al*., 2019; Ibáñez *et al*., 2019; Karavani *et al*., 2018). In the current context of climate change, climate components play a determinant role in successful regeneration particularly for seeding species, thus determining population resilience. Given that seedlings are highly sensitive to climatic stress, drought conditions during the first years after fire critically hampers their survival probability (Baudena *et al*., 2020; Davis *et al*., 2019; Henzler *et al*., 2018).

In the years following the emergence of seedlings, their growth into saplings and juveniles stages is determined by climatic conditions (de Luis *et al*., 2009; Fenner, 1987; Littlefield, 2019). For instance, regeneration may exhibit nonlinear responses to climatic fluctuations given the existence of thresholds in the relationship between demographic variables and climatic ones (vapour pressure deficit, maximum surface temperature) (Davis *et al*., 2019). In addition, microsite processes are important (Clark-Wolf *et al*., 2022). For instance, the presence of neighbouring plants modulates the development of saplings through inter or intraspecific competition for the resources (Martin-Benito *et al*., 2011; Ne'eman *et al*., 2004; Pausas *et al*., 2002). Also, ground surface properties (e.g., litter, bare clay, rocks, wood) and soil characteristics can generate microhabitats that may improve or diminish the response of recruits to local climatic conditions (Moya *et al*., 2020).

Species' environmental niche offers a powerful study framework to ecologically understand the response of recruiting populations to the climatic and microsite conditions occurring after wildfires, and to assess the implications for the fate of these populations in a climate change scenario (Larson *et al*., 2023). Numerous environmental factors (abiotic and biotic) intermix in defining species niche, but given the relevance of climate for plants (e.g., Schultz *et al*., 2022), climatic factors representing the species' climatic niche remains a dominant force for projecting ecological changes, especially under climate changes. The climatic niche can be inferred by translating the climatic characteristics of the sites where the species is present in the territory to an environmental space built with climatic variables. In spite of the resulting simplification of species' niche characteristics, this approach has proven to be robust enough to interpret the differential responses of concurrent woody species (Pérez-Navarro *et al*., 2024; Pérez-Navarro *et al*., 2019; Sapes *et al*., 2017) or populations of the same tree species across geographic gradients (Elvira *et al*., 2021; Lloret & Kitzberger, 2018; Margalef-Marrase *et al*., 2020) in the face of disturbance regimes or extreme weather events, such as heatwaves and droughts.

Pinus halepensis Mill. (Aleppo pine) is considered a well-adapted species to the relatively frequent fire regime and the seasonal water deficit conditions occurring in the Mediterranean region (Chambel *et al*., 2013). It is widely distributed in the Mediterranean basin, particularly in abandoned fields and burned areas. Some of the traits that may improve its post-fire resilience are its reproductive precocity (Fernández-García *et al*., 2019; González-De Vega *et al*., 2016; Tapias *et al*., 2004) and the presence of serotinous or semi-serotinous cones that conserve the viability of the enclosed seeds during at least three years and that open after high temperatures (Daskalakou & Thanos, 1996; Verkaik & Espelta, 2006). Although such traits may lead to a great regeneration success after wildfires, the eventual establishment of Aleppo pine populations exhibit a quite heterogeneous territorial pattern (Pausas, *et al*., 2004a; Rodrigo *et al*., 2004), which is likely determined by local conditions in terms of climate during the years previous and after the wildfire (Elvira *et al*., 2021), and by biotic interactions (e.g., seed predation, herbivory) (Ne'eman *et al*., 2004).

In this study, we aim to analyze the relationship between post-fire regeneration and climatic conditions relative to the species' climatic niche. Our main hypothesis is that, together with microsite characterisics, the position in niche space (distance to niche optimum and niche edge) after the fire will modulate recruits performace. We expect that the size of *P. halepensis* recruits, including height, basal area and crown size, will be lower when the climatic conditions after the wildfire has been closer to the drier limit of the species' climatic niche. Specifically, we study the size of *P. halepensis* recruits established after wildfires in nineteen burned areas of Catalonia (NE of Spain), also evaluationg the role of microsite characteristics (vegetation cover and soil stoniness). The climatic conditions of the years following establishment were characterized according to the species' climatic niche defined by *P. halepensis* occurrences across its European distribution range (Pérez-Navarro *et al*., 2020).

3.2 Material and methods

Study species

Pinus halepensis ranges in the Mediterranean Basin from the West (Spain, Morocco) to the East (Lebanon) (Mauri *et al*., 2016a). It is mainly present in thermo- and meso-Mediterranean areas, but it also inhabits lower altitudes in mountain regions close to the coast. *P. halepensis* is well adapted to the dry summer conditions characteristic of the Mediterranean climate (Chambel *et al*., 2013), which is expected to expand its area according to future climate change models. Therefore, the suitable climate area over the

Mediterranean Basin for *P. halepensis* is likely to increase in the next decades (Urli *et al*., 2014).

This species is a post-fire obligate seeder whose seed release is promoted by fire or high temperatures due to a massive heat-induced opening of the serotinous cones retained in the crown (Palmero-Iniesta *et al*., 2017; Tapias *et al*., 2004). This allows this pine to successfully regenerate after crown fires, which are partially promoted by the accumulated lower dead branches in *P. halepensis* trees that enhance the vertical distribution of fuel (Ne'eman *et al*., 2004). These traits, together with its pioneer character and colonizing ability, are likely promoting the expansion of their populations in the territory after fires, which also benefit from land abandonment (Sheffer, 2012; Zavala *et al*., 2000). However, the presence of moderates rains in autumn following the fire season is requiered for the success of post-fire regeneration of the species (De Luís *et al*., 2005; Mendel *et al*., 1997; Retana *et al*., 2002). Additionally, short intervals between wildfires jeopardize the long-term persistance of this species cause they require on average 15 years after the fire to accumulate a canopy seed bank large enough to recover from fires (Macias *et al*., 2006).

Study area and sampling design

We sampled nineteen sites along the Catalonia territory (NE Spain) that burned only once between 2003 and 2014 (Figure 3.1, Supplementary Material, Table SM3.1). All sampling sites corresponded to *P. halepensis* forests before wildfire, as recorded in the closest plots of the Spanish National Forest Inventory IFN1 and IFN2 (Villaescusa & Díaz, 1998). By sampling sites affected only by one fire, we avoided the detrimental effects of high-fire recurrence on post-fire seed bank availability (Eugenio *et al*., 2006; Eugenio & Lloret, 2006; Santana *et al*., 2014). Recruitment density in each site was obtained from a previous survey (Elvira *et al*., 2021) or from specific surveys carried on for this study following the same protocols (please see Chapter 2 for details of the procedure).

In each site, we randomly established transects of aproximately 20 m in a number proportional to the burned area, and sampled the closest *P. halepensis* recruit every 2 m along the transects. In total, 45 transects were performed (mean number of transects per fire: 2.4, ranging from one to three) and 385 pines were destructively collected (mean number of pines per fire: 20.2, ranging from 5 to 30 pines per fire). Transects were located more than 100 m away from the fire edge (unburned forest) to avoid the contribution of seeds subsequently arriving after fire from surviving trees outside of the wildfire perimeter (Broncano *et al*., 2005). We collected plants with a basal area lower than 12 cm^2 and a height lower than 1.60 m to avoid the potential inclusion of small trees surviving from the fire. Root collar sections of the collected plants were used to determine the year of germination following standard dendrochronological techniques. Samples were air dried and successive polishing with progressively finer sandpaper was performed until tree ring limits were clearly visible under a stereo microscope to assign a calendar year to each ring from the bark to the pith.

For each collected plant we measured a set of size-related variables describing plant growth after its establishment following wildfire: height, basal area, diameter of the crown (average of the maximum projection and its perpendicular line) and percentage of green canopy. Also, we characterized biotic and abiotic microsite conditions potentially affecting recruits' growth. In a circumference of 1 m diameter around each sampled recruit, we estimated the percentage of projected cover of other *P. halepensis* individuals, and of the most dominant shrub (*Quercus coccifera*) and herbs (*Brachypodium retusum*) that could compete with pine juveniles. We also typified the soil surface properties within the 1 m diameter area through a stoniness index defined as $RCI = (Cl\,I * 0.25 + Cl\,II * 0.5 + Cl\,III * 0.75 + Cl\,IV) * 100^{-1}$, where *Cl , Cl II, Cl III and Cl IV* corresponds, respectively, to rocks or stones with a diameter ≤1.5 cm, between 1.6-7 cm, between 7.1-15 cm, and ≥15.1cm, being the four *Cl* classes measured as cover percentage.

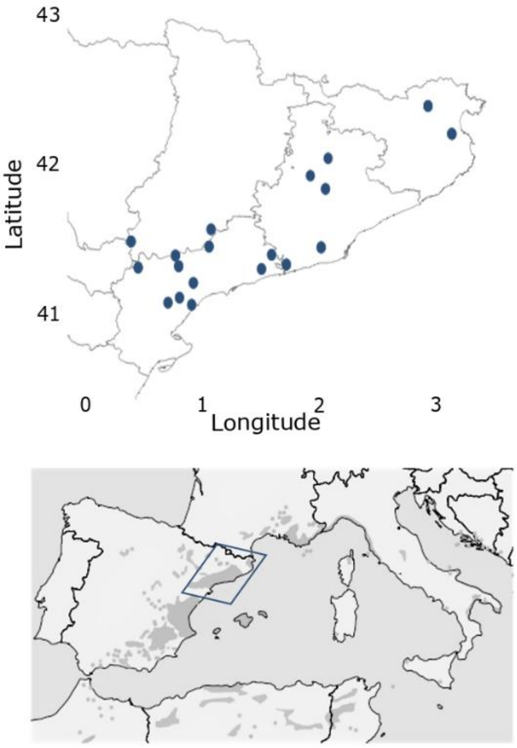


Figure 3.1: Location of sampling sites (N = 19) of *Pinus halepensis* regeneration after wildfire in Catalonia, NE Spain. The inset map shows the distribution area of *P. halepensis* (shaded grey) in the western Mediterranean Basin (modified from Fady *et al*., 2003).

Climatic niche characterization of P. halepensis

We characterized *P. halepensis* climatic niche according to its European distribution range using monthly climatic data obtained from CHELSA (Karger *et al*., 2017, period 1979-2018). Following Pérez-Navarro *et al*., 2020, we extracted twelve bioclimatic variables from all the geographic locations in which the species was recorded as the dominant species in the high-resolution, pan-European tree occurrence inventory (EUForest -Mauri *et al*., 2016b). We included 13121 occurrences distributed across Croatia, Cyprus, France, Greece, Italy, Portugal and Spain (12298 of them in Spain). We extracted yearly climate values instead of the average values of the period 1979-2018 to better characterize the inter-annual variability in the environmental conditions experienced by the species (Pérez-Navarro *et al.*, 2020).

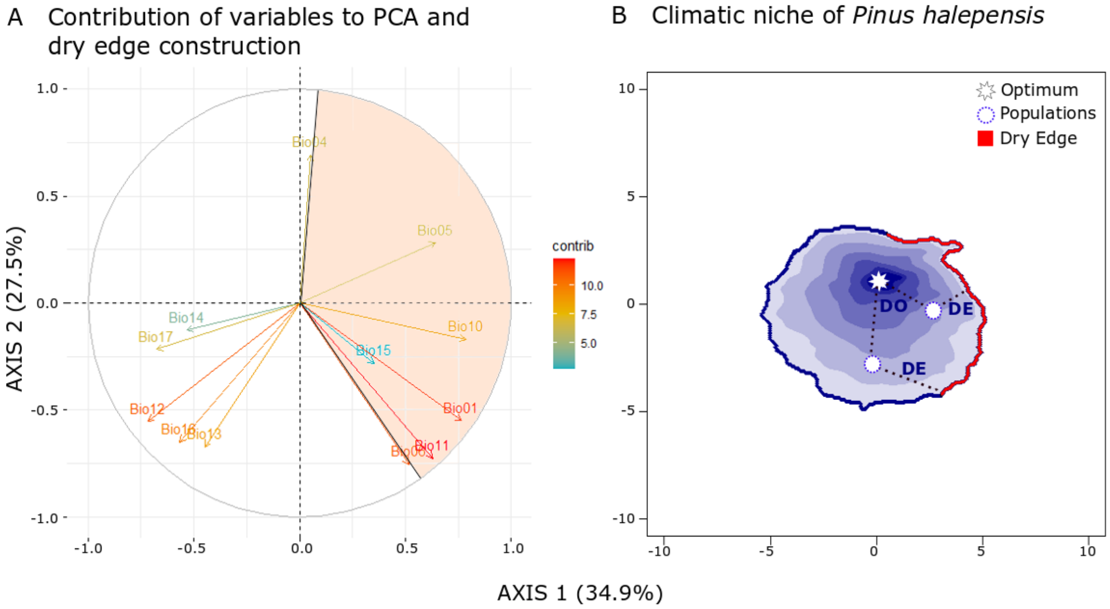
First, using the 6140628 climatic records obtained from the EU-level *P. halepensis* geographical occurrences (13121 occurrences * 12 bioclimatic variables * 39 years of the 1979-2018 period) we built an environmental climatic space through principal component analysis (PCA). The projected inertias of PCA axis 1 and 2 were 34.9 % and 27.5%, respectively (Figure 3.2A). The first PCA axis was positively related with the annual mean temperature (Bio1), the mean temperature of warmest quarter (Bio10) and the annual precipitation (Bio12), and negatively related with the maximum temperature of warmest month (Bio5) and the precipitation of driest quarter (Bio17). The second PCA axis was positively related with the minimum temperature of coldest month (Bio6), and negatively related with the mean temperature of coldest quarter (Bio11), the precipitation of wettest quarter (Bio16) and the precipitation of wettest month (Bio13) (Figure 3.2A).

Then, we translated the values of the 6140628 climatic records corresponding to *P. halepensis* occurrences to the climatic space generated by the PCA axes. The density of occurrences within this climatic space was computed through kernel density estimates, representing an estimation of the *P. halepensis* realized climatic niche (Broennimann *et al.*, 2012). The species climatic optimum (Figure 3.2B), was computed as the centre of mass of *P. halepensis* density occurrence in the climatic space. The distribution limit of the species' occurrence in the climatic space, which would correpond to the niche edge, was calculated using the kernel encompassing 95% of the observations.

Niche metrics for recruiting trees

The greographic location for each of the 19 sampling sites included in this study were used to obtain the annual values of the 12 bioclimatic variables for the period between the year of the fire in each site and 2018. These data were translated into the environmental PCA space used to define *P. halepensis*' climatic niche. We selected some bioclimatic variables to interpret the characteristics of the edge - obtained from the PCA - in its different contour sections, that is, which are the climatic conditions that characterize each section of the contour delineating the niche edge. Accordingly, we defined a dry edge (Figure 3.2) characterized by high temperatures and seasonality (positive contribution of Bio 1, 4, 5, 6, 10, 11 and 15) and low precipitation (negative contribution of Bio 12, 13, 14, 16 and 17). Using the optimum as a relative centre, the projection of the bioclimatic variables Bio 4 (temperature seasonality) and Bio 6 (mean daily minimum air temperature of the coldest month) on the niche contour were used to define the dry edge of the species' climatic niche

(Figure 3.2). We selected the dry edge as a reference to interpret the performance of *P. halepensis* recruits because drought conditions represents the main climatic limitation in the Mediterranean ecosystems.


A Contribution of variables to PCA and dry edge construction

B Climatic niche of *Pinus halepensis*

Figure 3.2. A: correlation circle obtained from the principal component analysis (PCA) performed with twelve bioclimatic variables describing the climatic conditions for the period 1979-2018 in the geographical locations in which *Pinus halepensis* has been recorded across Europe. Arrows' colours indicate the contribution of each variable. Red shaded area indicate the projection of the variables considered to define the dry edge of the species niche (see Methods). B: Environmental climatic space or the realized climatic niche of *P. halepensis* and the dry edge of the niche (red portion) within the environmental space defined by the PCA axes, including two population examples. DO: Distance to niche optimum, DE: Distance to the closest point of the dry edge of the niche.

Subsequently, sites' yearly locations within the climatic niche were used to calculate the Euclidean distance to the niche optimum and to the closest point of the dry edge of the climatic niche (Figure 3.2B). For each sampled recruit within a site, niche metrics were computed for each year within the period comprised between its recruitment year and 2018. Finally, we calculated the mean value and the standard deviation of the distances to the niche optimum and the dry edge of the niche for each sampled tree, as well as the minimum distance to the niche optimum and to the dry edge. Such computations characterize the averaged climatic suitability and its variability, in relation to the species' climatic niche, as well as estimations of extreme favourable and unfavourable climatic conditions (i.e., minimum distance to the niche optimum and to the niche edge respectively) during the life of the recruiting pines. Note that distances to niche optimum and to the dry edge for any given point within the niche are not complementary due to the asimetry of the *P. halepensis* climatic niche.

R package ade4 (version 1.7-22, Dray & Dufour, 2007) were used to compute the PCA. R packages ks (version 1.10.7, Chacón & Duong, 2018) and SDMTools (version 1.1-221, van der Wal *et al*., 2014) were used for characterizing *P. halepensis* climatic niche and to compute distances to the optimum and to dry edge.

Statistical analyses

Generalized linear mixed models (GLMM) with normal distributions were used to assess the relationship between each of the recorded size-related variable of recruiting pines – response variables: height, basal area, crown diameter and percentage of green canopy – and the predictor variables, including position within the species' climatic niche – mean, maximum, minimum and standard deviation of distances to the niche optimum and to dry edge of the niche - for each recruit, and recruits' microsite conditions – RCI and *P. halepensis*, *Q. coccifera* and *B. retusum* cover –. All predictor variables were standardized by subtracting their mean value and diving by their standard deviation prior to model fitting (Supplementary Material, Table SM3.2). Four sets of models, one for each size variable, were performed. Final models were selected according to the stepwise selection procedure based on the Akaike information criterion (AIC) and the explanation capacity (squared R), using the dredge function of MuMIn R package (version 1.48.4, Bartoń, 2019).

All statistical analyses were performed in R version 4.3.0 (R Core Team, 2024).

3.3 Results

Most recruits established one to three years after wildfire across burned sites although intrasite variability was small. The height of sampled juveniles ranged between 0.25 m and 3.22 m, with a mean value of 1.18 m (standard deviation SD = 0.54); basal area showed values between 0.21 cm^2 and 46.81 cm^2, with a mean of 5.29 cm^2 (SD = 6.04); crown diameter ranged between 10.0 cm and 165.0 cm, with a mean value of 65.0 cm (SD = 29.53); percentage of green canopy estimations were between 10.0% and 100.0%, with a mean of 75.7% (SD = 17.72).

Final models (Figure 3.3) show that the height of *P. halepensis* recruits was significantly taller in locations with average climatic conditions after the fire more distant to the dry edge of the species' climatic niche (i.e., positive relationship between recruits height and mean distance to the dry edge of the niche, p-value < 0.05; Figure 3.3A; Supplementary material, Table SM3.3), and Older individuals older (p-value <0.001) and those with higher cover of neighbouring conspecific pines (p-value <0.001) were also taller. Tree height was also significantly lower in pines surrounded by rocks and big stones (i.e., negative relationship with RCI, p-value < 0.01) and a marginaly significant, negative relationship was found with the minimum distance to dry edge of the niche (i.e., minimum distance to dry edge estimated from yearly climatic conditions, p-value < 0.1). The distance to niche optimum showed a positive but non-significant relationship with tree height.

Basal area was significantly larger in older recruits (p-value <0.001, Figure 3.3B; Supplementary material, Table SM3.4). Neither niche distance metrics nor microsite characteristics had a significant effect on basal area. Crown diameter was also significantly larger in older plants (p-value <0.001, Figure 3.3C; Supplementary material, Table SM3.5), and in recruits with lower cover of neighbouring conspecific pines (p-value < 0.05). The percentage of green canopy of the recruits was only significantly and negatively related with the cover of neighbour recruiting pines (p-value <0.001; Figure 3.3D, Supplementary material, Table SM3.6). The proportion of green canopy exhibited a non-significant, negative relationship with the mean distance to the niche optimum.

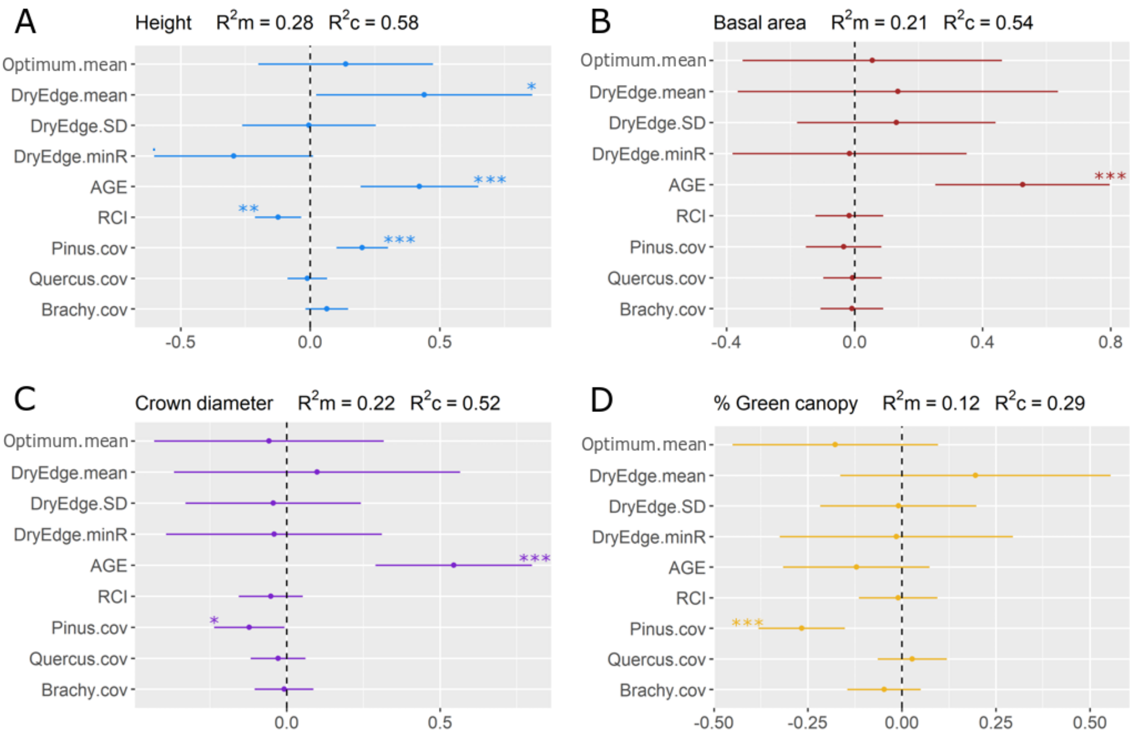


Figure 3.3: Final models (only fixed effects are shown) for each of the four assessed size-related variables of recruiting *Pinus halepensis*. A) Height, B) Basal area, C) Crown diameter, D) Green canopy percentage. In all subplots, ***p-value <0.001, ** p-value < 0.01, * p-value < 0.05, · p-value < 0.1.

3.4 Discussion

We show that recruits performance in post-fire regeneration of *P. halepensis*, a representative, fire adapted Mediterranean conifer tree, is modulated by the location of individuals within the species' realized climatic niche (distance to the niche optimum and the dry edge of the niche) associated to the climatic conditions after fire. Tree age and microsite conditions such as soil rockiness and the influence of conspecific recruits also appears among the factors influencing the growth of recruiting pines. Specifically, newly established *P. halepensis* individuals after wildfire benefit from inhabiting more suitable climatic conditions (i.e., wetter locations far away from the dry edge) relative to the species' climatic niche: recruits growing in sites with climatic conditions on average more distant to the dry edge of the niche are higher. However, our results suggest that the occurrence of years with extremely favourable climatic conditions (e.g., minimum distance to niche optimum) does not improve growth performance. In fact, contrary to our expectations, recruits' height tend to be higher in sites where transitory conditions close to the dry edge of the climatic niche occurred (negative relationship between tree height and the minimum distance to the dry edge of the niche). Microsite conditions surrounding the recruits are also relevant to explain recruits height, crown size and the percentage of green canopy: higher stoniness results in lower height, while the presence of surrounding conspecific recruits results in taller recruits, but with smaller crown and less percentage of green canopy. No significant effect of the shrub *Q. coccifera* or the herb *B. retusum* was found for any of the assessed size related traits of the recruits, suggesting that their competitive impact would mainly operate at earlier stages (e.g., germination phase) of *P. halepensis* establishment.

The relevance of niche metrics (distance to niche optimum and to the dry edge) in explaining recruits performance is contingent on the assessed trait. Plant height emerged as the most sensitive growth-related variable in relation to niche position (i.e., environmental conditions since the year of establishment), likely due to its greater plasticity than basal area and crown size, which appeared significantly affected by tree age (i.e., older recruits have larger basal area and crown size) while also integrating the effects of the climatic conditions since the year of establishment. By contrast, green canopy seem to respond to environmental drivers operating at shorter-time scales, and appeared particularly sensitive to competence with neighbouring pines (crown cover of neighbour pines).

The higher height of recruits growing in localities that, on average, are more distant from the dry edge of the species' climatic niche is consistent with the premise that less favorable climatic conditions jeopardize the primary growth of the saplings established after disturbances (Margalef-Marrase *et al.*, 2022; Pausas *et al.*, 2004b; Sapes *et al.*, 2017). Green canopy percentage also exhibited better performance in locations with more favourable climatic conditions for the species. This trend was reflected by a negative correlation with the mean distance to the climatic niche optimum and a positive relationship with the distance to the dry edge of the niche, although these relationships appeared not significant, likely due to the high level of variability among recruits. However, years with extreme conditions (i.e., minimum distance to the dry edge of the niche) were related with higher height of the recruits. A potential mechanism related to this findings could be that extreme conditions act as a filter for the less vigorous individuals within the recruiting population, reducing intraspecific competition. Reduced competence would allow surviving pines to allocate more resources to growth, thus promoting taller recruits (Alfaro-

Sánchez *et al.*, 2015). So, individuals would show a high primary growth rate mediated by overcompensation processes, an intraindividual mechanism that can operate after unfavourable conditions (Li *et al*., 2021).

Microsite conditions, including both biotic and abiotic factors appear also as key factors for recruits performance, in agreement with recent recruitment niche frameworks (Larson *et al*. 2023). From the one hand, higher presence of conspecific individuals significantly modulated plants height, crown size and crown greeness, indicating that intra-specific competition modulate the structural characteristics of post-fire regeneration. In an heliophilous species such as *P. halepensis* a higher density of neighboring conspecific pines promote taller recruits with smaller crown diameter and with a lower degree of canopy greeness. This competition for light is likely to be reduced over the years because of mortality of juveniles due to self-thinning in dense populations (Brunet-Navarro *et al*., 2016). On the other hand, surface stoniness (estimated by RCI), which could represents lower amount of available soil (and therefore of nutrients and water) for young plants (Preisler *et al.*, 2019), was negatively and significantly related to sapling height. Similarly, stoniness also exherted a negative effect on crown size, although to a lesser degree and not significant in our models. Both relationships may reflect less favourable microsite conditions for recruits performance in stony soils, which modulate the influence of larger scale environmental factors than those assessed here (Astudillo-Sánchez *et al*., 2019).

Overall, our findings highlight, in agreement with previous works (e.g., Batllori *et al*., 2019; Baudena *et al*., 2020; Davis *et al*., 2019), the importance of post-fire climatic conditions among the mechanisms modulating ecosystems resilience. However, in our approach, the lack of a comprehensive inventory for *P. halepensis* in the Mediterranean Basin may have underestimated the climatic niche of the species, especially a the hotter-dry edge. Although EUforest is a notable initiative to build a common datase for European tree species (Mauri *et al*., 2016b), niche modelling for Mediterranean species would requires information of their occurrence in the Northern Africa territories in order to obtain a complete estimation of their climatic distribution. In addition, the differences in the frequency of sampling, plot dimensions and survey protocols may increase undesired variability when using the EUForest data base. In addition, the use of adult tree occurrences to compute the climatic niche may not entirely reflect the environmental requirements - translated to niche estimations - of recruiting plants (Larson *et al*., 2023). Nevertheless, since most of the occurrence data (94%) comes from forest inventories within the study area (Spain) and we focussed on relatively consolidated individuals (i.e., not initial germination stages), we believe that our approach allows a meaningful characterization of the niche optimum and dry edge conditions of the *P. halepensis*' climatic niche and their influence on post-fire recruits performance.

The results presented here report for the first time the usefulness of the species climatic niche framework to understand demographic responses at the recruit individual level after fire. This expands pevious reports of the influence of the position in climatic niche space in modulating response to disturbances at the population level. For instance, an assessment of regeneration density of *P. halepensis* in the same set of burned sites revealed that deviations from the optimunm of the climatic niche reflecting warmer temperatures after the fire were negatively related to recruits density (Elvira *et al*., 2021 i.e., Chapter 2). Similarly the relationship between position in the climatic niche and population response to other disturbances have been found for shrublands and forests experiencing die-off under extreme drought, in some cases concurrently affected by bark beetles (e.g., Jaime *et al*., 2019, 2022; Margalef-Marrase *et al*., 2020; Pérez-Navarro *et al*., 2019). The individual-level analysis presented here, together with the population-level responses outlined above, emphasize the climatic niche as a powerful framework towards better understanding the ecological influence of disturbances and post-disturbance recovery in the context of climate change.

3.5 Conclusions

The location of the population of *P. halepensis* within the realized species' climatic niche and specifically in relation to the dry edge of the niche - reflecting warmer and drier conditions - appear as suitable metrics to explain the post-fire performance of recruits in Catalonia populations. Primary growth (i.e., height) is the resilience metric that results more conditioned by the position within the niche, compared with the other metrics such as basal area, diameter of tree crown and percentage of green canopy. Drier conditions after fire result in smaller recruits although the presence of dry pulses (i.e. years of extremely dry conditions) produce higher height of the regeneration cohort, probably because of the filtering effects that allow access to more resources for surviving recruits. Microsite characteristics such as soil surface stoniness or intraspecific competition also exert a significant influence on recruits' performance and thus on ecosystem resilience.

Suplemantary material

Table SM3.1: Sampling site location, year of fire, and average post-fire density of regeneration (pines/ha).

		ID	YEAR	SITE LOCALITY	UTM			DENSITY
CATALONIA	BARCELONA	19132	2006	HOSPITALET DE L'INFANT	31T	321160	4539889	1428.6
		19218	2013	VALLIRANA	31T	412193	4580128	2897.92
		19351	2005	VILLAFRUNS	31T	405582	4632253	625
		19510	2012	ST FELIU SASSERA	31T	418009	4644739	2068.966
		19512	2012	PANT. DE FOIX	31T	387941	4567971	1686.78
		19554	2003	TALAMANCA	31T	415341	4622714	439.47
	GIRONA	19486	2005	VILARIG	31T	487051	4682408	6045.77
		19568	2006	GARRIGOLES	31T	503500	4662039	22373.91
	LLEIDA	19537	2003	ESPLUGA CALVA	31T	335976	4594431	3541.66
		19542	2003	GRANJA ESCARPE	31T	280064	4587023	1873.935
	TARRAGONA	19181	2005	BELLAGUARDA	31T	310876	4575914	3924.3
		19185	2009	ST JAUME	31T	377764	4575113	3214.28
		19187	2002	BONASTRE	31T	370565	4564879	4750
		19297	2002	TIVISSA	31T	312480	4545260	4929.01
		19330	2014	RASQUERA	31T	304579	4541811	2380.95
		19386	2007	PARC EOLIC	31T	322462	4555577	2284.53
		19407	2005	RIBA-ROJA D'EBRE	31T	284489	4567667	5298.59
		19534	2006	RIUDABELLA	31T	334164	4581879	42822.26
		19668	2012	CABACES	31T	312679	4567974	35069.26

Table SM3.2: Variability of climatic niche and individual related characteristics. (standardized values with raw values within brackets).

FACTOR		MEAN	MIN	MAX	SD
DISTANCE TO OPTIMUM	MEAN	0.000 (2.696)	-1.6997 (1.177)	1.6696 (4.189)	1.000 (0.868)
	MINIMUM	0.000 (1.4189)	-1.3492 (0.1875)	1.5526 (2.836)	1.000 (0.870)
	SD	0.000 (0.9322)	-1.4441 (0.4582)	3.4944 (2.0794)	1.000 (0.385)
DISTANCE TO EDGE	MEAN	0.000 (2.0587)	-1.9825 (0.9768)	1.5717 (2.9164)	1.000 (0.832)
	MINIMUM	0.000 (0.9062)	-1.3754 (0.0478)	1.6470 (1.9340)	1.000 (0.625)
	SD	0.000 (0.7838)	-2.4834 (0.2035)	2.2799 (1.3166)	1.000 (0.329)
RCI (ROCK COVER INDEX)		0.000 (0.3739)	-0.7813 (0.250)	3.6344 (0.950)	1.000 (0.158)
PERCENTAGE OF COVERTURE	P. HALEPENSIS	0.000 (18.28)	-0.7161 (0.000)	3.0051 (95.00)	1.000 (25.527)
	Q. COCCIFERA	0.000 (6.419)	-0.4014 (0.000)	5.2264 (90.00)	1.000 (15.991)
	B. RETUSUM	0.000 (13.29)	-0.6407 (0.000)	3.6969 (90.00)	1.000 (20.742)
AGE		0.0000 (11.73)	-1.9918 (5)	1.8576 (18)	1.000 (3.378)

Table SM3.3: Model for height considering all variables: AIC = 901.79, BIC = 949.10; Marginal pseudo-R² (fixed effects) = 0.28, Conditional pseudo-R² (total) = 0.58. p values calculated using Satterthwaite d.f.

PREDICTORS	ESTIMATES	CI	P-VALUE
(INTERCEPT)	0.00	-0.28 – 0.28	0.997
OPTIMUM MEAN	0.14	-0.20 – 0.47	0.424
DRYEDGE MEAN	0.44	0.02 – 0.86	**0.038**
DRYEDGE SD	-0.00	-0.26 – 0.25	0.972
DRYEDGE MIN	-0.30	-0.60 – 0.01	0.059
AGE	0.42	0.19 – 0.65	**<0.001**
RCI	-0.12	-0.21 – -0.03	**0.007**
P. HALEPENSIS COVER	0.20	0.10 – 0.30	**<0.001**
Q. COCCIFERA COVER	-0.01	-0.09 – 0.07	0.781
B. RETUSUM COVER	0.06	-0.02 – 0.15	0.124

Table SM3.4: Model for basal area considering all explanatory variables: AIC = 1030.70, BIC = 1078.02, Marginal pseudo-R² (fixed effects) = 0.21, Conditional pseudo-R² (total) = 0.54. p values calculated using Satterthwaite d.f

PREDICTORS	ESTIMATES	CI	P-VALUE
(INTERCEPT)	0.10	-0.24 – 0.43	0.575
OPTIMUM MEAN	0.06	-0.35 – 0.46	0.789
DRYEDGE MEAN	0.14	-0.36 – 0.64	0.595
DRYEDGE SD	0.13	-0.18 – 0.44	0.409
DRYEDGE MIN	-0.02	-0.38 – 0.35	0.934
AGE	0.53	0.25 – 0.80	**<0.001**
RCI	-0.02	-0.12 – 0.09	0.760
P. HALEPENSIS COVER	-0.03	-0.15 – 0.08	0.571
Q. COCCIFERA COVER	-0.01	-0.10 – 0.08	0.886
B. RETUSUM COVER	-0.01	-0.11 – 0.09	0.872

Table SM3.5: Model for crown diameter considering all explanatory variables: AIC = 1005.26, BIC = 1052.57, Marginal pseudo-R² (fixed effects) = 0.22, Conditional pseudo-R² (total) = 0.52. p values calculated using Satterthwaite d.f

PREDICTORS	ESTIMATES	CI	P-VALUE
(INTERCEPT)	0.05	-0.26 – 0.36	0.742
OPTIMUM MEAN	-0.06	-0.43 – 0.32	0.761
DRYEDGE MEAN	0.10	-0.37 – 0.57	0.676
DRYEDGE SD	-0.04	-0.33 – 0.24	0.762
DRYEDGE MIN	-0.04	-0.39 – 0.31	0.817
AGE	0.54	0.29 – 0.80	**<0.001**
RCI	-0.05	-0.16 – 0.05	0.326
P. HALEPENSIS COVER	-0.12	-0.24 – -0.01	**0.038**
Q. COCCIFERA COVER	-0.03	-0.12 – 0.06	0.541
B. RETUSUM COVER	-0.01	-0.10 – 0.09	0.860

Table SM3.6: Model for green percentage considering all explanatory variables: AIC = 1024.94, BIC = 1072.26, Marginal pseudo-R² (fixed effects) = 0.12, Conditional pseudo-R² (total) = 0.29. p values calculated using Satterthwaite d.f

PREDICTORS	ESTIMATES	CI	P-VALUE
(INTERCEPT)	0.01	-0.20 – 0.22	0.899
OPTIMUM MEAN	-0.18	-0.45 – 0.10	0.204
DRYEDGE MEAN	0.20	-0.16 – 0.56	0.286
DRYEDGE SD	-0.01	-0.22 – 0.20	0.931
DRYEDGE MIN	-0.01	-0.32 – 0.30	0.926
AGE	-0.12	-0.32 – 0.07	0.222
RCI	-0.01	-0.11 – 0.09	0.858
P. HALEPENSIS COVER	-0.27	-0.38 – -0.15	**<0.001**
Q. COCCIFERA COVER	0.03	-0.06 – 0.12	0.552
B. RETUSUM COVER	-0.05	-0.15 – 0.05	0.341

Chapter 4

Post-fire regeneration is modulated by the position in the realized climatic niche in three Mediterranean tree species

Abstract

Understanding how climatic conditions and fire severity affect the post-fire regeneration of Mediterranean vegetation is key to understanding populations resilience in a context of increasingly large wildfires with higher intensity and magnitude, and more intense drought-related conditions due to climate change. We use as system study three tree species (*Pinus halepensis*, *Quercus ilex* and *Pinus nigra*) widely distributed in the Mediterranean Basin, with different post-fire regenerative strategies (seeder, resprouter and fire-sensitive, respectively). We aim to analyse how climatic conditions preceding and posterior to fire, relative to the species' climatic niche, and fire severity influence post-fire regeneration. We characterized the species' realized climatic niche from their records in the EU Forest Inventory, overlapping locality occurrences with the respective yearly values of 12 bioclimatic variables for the period 1979-2018. After obtaining an environmental space defined by the PCA axis built from the bioclimatic variables, Kernel density estimates were applied to determine the species' climatic niche optimum and edge. We also interpreted the bioclimatic variables in the PCA to compute the wet and dry edges of the climatic niche. We selected those plots in the Spanish National Forest Inventory (IFN), in which the three studied species were dominant in IFN2 and that were burned between the IFN2 and IFN3 successive samplings. Then, we extracted the identity of the dominant species and the canopy cover before and after fire. Subsequently, we modelled changes in species dominance (species shift) and the recovery of canopy cover in relation to the distance to the respective species' climatic niche optimum and to the wet and dry edges of the niche in the burned plots locations, before and after the fire. We also included fire severity as an explanatory factor in the models. Our assessment reveals that the climatic conditions relative to the climatic niche before and after fire modulate the short-term resilience to fires. *P. halepensis* tends to maintain better its dominance in average pre- and post-drier conditions within its climatic niche, although larger canopy recovery was also observed in wet conditions. *Q. ilex* appeared to require post-fire humid conditions within its climatic niche to remain dominant. *P. nigra* tends to be replaced after wildfires, although post-fire years with climate conditions near the species' s wet edge may occasionally promote its maintenance as dominant. Fire severity significantly explained the shift of dominant species in *P. nigra* and *Q. ilex* plots, but not in *P. halepensis* ones, supporting the notion that the

latter is well adapted to stand-replacing wildfires. The study reveals that the position within the climatic niche, together with fire severity, offers a suitable framework to understand post-fire regeneration patterns in Mediterranean tree species.

4.1 Introduction

Forest wildfires are one of the main natural drivers of Mediterranean-type ecosystems and landscapes, modifying the structure and composition of vegetation. In the Mediterranean Basin, the characteristics of fire regimes have been altered in terms of frequency, size, seasonality, and severity (Chergui *et al*., 2017; Keeley *et al*., 2013; McLauchlan *et al*., 2020) in recent decades. This is partially due to increased temperatures and changes in the precipitation regime that, especially in summer, lead to severe drought that pushes wildfires outside their historical record (Alvarez *et al*., 2024; IPCC, 2023; Ozturk *et al*., 2015; Spinoni *et al*., 2018). Furthermore, the socioeconomic changes involving rural abandonment and changes in traditional land use have increased the amount and continuity of fuel that can burn (Chergui *et al*., 2017), thereby increasing the intensity and the extent of wildfires.

Fire, as a disturbance, has been an evolutionary force leading to fire-adapted systems, in which plant life history and reproductive traits allow species to remain in secular fire regimes (Beckage *et al*., 2009; McLauchlan *et al*., 2020). In these systems, some of the traits that improve plant fitness correspond to fire-stimulated flowering, seed storage in closed fruits (serotinity), fire-stimulated germination, bud protection, and shoot sprouting (Gill, 1977; Lamont & He, 2017).

In the Mediterranean Basin, there are two dominant fire-recovery strategies: on the one side, seeder species, with abundant seedling recruitment after fire, focus their reproductive effort on seed production; on the other side, resprouter species exhibit vegetative growth from surviving parental tissues such as roots, rhizomes or lignotubers (Pausas & Keeley, 2014). Yet, these strategies are not mutually exclusive but rather represent the extremes of a gradient of post-fire responses. So, plant species can show one of these obligate responses, exhibit both of them (facultative species) or remain outside the regenerative strategy gradient, being their fire-sensitive populations dependent on colonization processes (colonizers) (Keeley, Bond, *et al*., 2011). Eventually, the balance of the relative costs and benefits of the regeneration strategies and fire regimes including severity, frequency and seasonality can differentially modify population demographic rates (Pausas & Keeley, 2014).

Recent changes in fire behaviour in the Mediterranean Basin, with a greater frequency of high-intensity fires (Aldersley *et al*., 2011, Alvarez *et al*. 2024), in some cases resulting in very large forest wildfires, have been related to increasing drought (Chergui *et al*., 2017; Ordóñez *et al*., 2005). Large extents of severely burned land can limit tree regeneration after fire, even for fire-adapted species. This may be due in sprouting species to the destruction of protected buds and reserves, and in seeding species to the depletion of seed banks, or long distances from seed sources in unburned trees, especially in remaining forested patches (Davis *et al*., 2019; Karavani *et al*., 2018; Ordóñez *et al*., 2005). Regeneration failure after fire can therefore disrupt ecosystem resilience (engineering resilience, sensu Holling, 1996), which is recognized as the capacity of a system to return to the previous state after disturbance (Pimm, 1984). So, forest resilience after fire can be estimated in terms of the density of regeneration (Elvira *et al*., 2021 i.e., Chapter 2), the growth of recruiting cohorts (Chapter 3), or the relative abundances of species in the community (Odland *et al*., 2021), among others.

In addition to fire regime characteristics, post-fire climatic conditions can determine the success of tree regeneration (Batllori *et al*. 2019; Baudena *et al*. 2020), including both the establishment and the growth of trees (Karavani *et al*., 2018). Climatic conditions can be characterized through the climatic niche, which offers an appropriate framework to asses species' response to disturbance (Díaz-Borrego *et al*., 2024; Jaime *et al*., 2019; Margalef-Marrase *et al*., 2022). Therefore, regeneration success after fires will depend on the location of the population in the climatic niche of the species (Elvira *et al*., 2021; Pérez Navarro *et al*., 2018). For instance, populations historically located near the edge of the climatic niche are expected to tend to show poorer regeneration. In contrast, those species growing in conditions closer to the niche optimum are expected to perform better in terms of regeneration and growth (Margalef-Marrase *et al*., 2020, Chapter 3).

This study aims to assess whether the populations' position in the climatic niche space affects the post-fire resilience of three dominant tree species in the western Mediterranean Basin, *Pinus halepensis*, *Quercus ilex* and *Pinus nigra*, and to what degree their regeneration strategy (seeding, resprouting and fire-sensitive, respectively) is determinant for such response. For this purpose, we analyse the short-term resilience of the study species to wildfires across their biogeographical range in Spain, aiming to assess the role of pre- and post-fire climatic conditions relative to the species' climatic niche. We characterized resilience after fire as the capacity of a given tree species to remain as the dominant one, and as the efficiency in recovering the canopy cover. For each species, the distance of burned populations to the respective climatic niche optimum (i.e., niche core or centroid) and to the climatic niche edge was used to characterize pre- and post-fire climate conditions. Our main hypothesis is that the position of the populations in the niche space (i.e., distance to niche optimum and edge) will modulate their resilience to fire, having better recovery capacity those populations growing in locations close to the niche optimum and far from the dry edge of the species niche. Also, we expect that the relationship between populations' position in the niche space and recovery patterns, will be determined by the species regeneration strategy.

4.2 Material and methods

Species of study

We studied three of the most common tree species of Mediterranean forests in the Iberian Peninsula, which are representative of distinct regeneration strategies in front of wildfires. *Pinus halepensis* Mill is an obligate seeder that persists through effective recruitment of seedlings, *Quercus ilex* L. resprouts after the fire and *Pinus nigra* J.F. Arnold is a fire-sensitive species that does not have an effective strategy to persist, thus being obligated to colonize burned sites from surviving trees in unburned patches. Aleppo pine (*P. halepensis*) is the most thermophilic and abundant pine in the Mediterranean climate in the western Mediterranean Basin (Rouget *et al.*, 2001), with growth (since it is a light-demanding species) and reproductive behaviour highly conditioned by fire regimes. It produces serotinous and semi-serotinous cones that accumulate a crown seed bank that is released by wildfires, and supplies a high number of seeds (Climent *et al.*, 2008). Holm-oak (*Q. ilex*) is well-adapted to hot, dry summers, as well as to the relatively harsh winter conditions found in some locations in the Mediterranean Basin (Bussotti *et al.*, 2014), although extreme drought events can affect more this species than other evergreen trees (Pollastrini *et al.*, 2019). The underground parts of holm-oak survive wildfires and provide the resources to the dormant buds to resprout vigorously afterwards (Clarke *et al.*, 2013; Retana *et al.*, 1992). Black pine (*P. nigra*) is the northernmost of the three studied species. After a wildfire, it requires the arrival of seeds from unburned areas to regenerate (Espelta *et al*., 2002).

Plot sites selection

Using the fire database compiled by Alvarez *et al*. (2024) we obtained the perimeters of the fires in Spain between 1986 and 2018. We selected those plots in the Spanish National Forest Inventory (IFN), included within the fire perimeters, in which the three studied species were dominant (canopy cover ≥ 50%) and that were burned only once between the successive samplings of IFN2 (1986-96, Villaescusa & Díaz, 1998) and IFN3 (1997-07, Bombín & Cezón, 2018) (Figure 4.1). We obtained 644 plots for *P. halepensis,* 107 for *Q. ilex* and 225 for *P. nigra.*

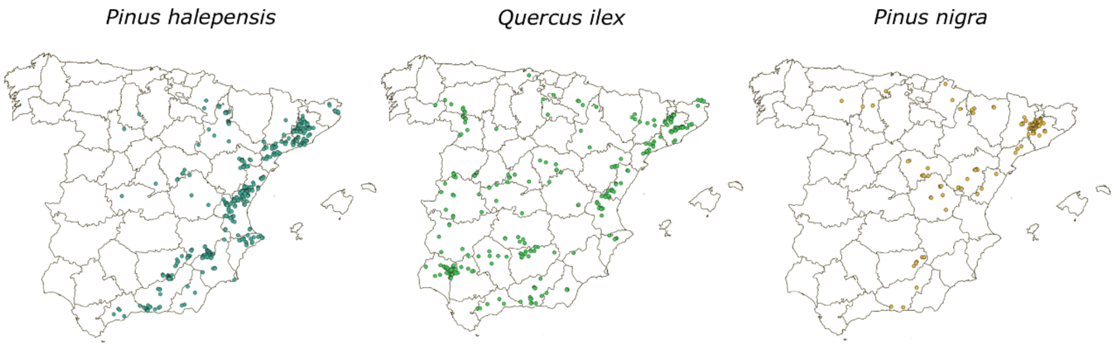


Figure 4.1: Location of burned plots across Spain which were dominated by the three species under study.

Resilience metrics

We assessed if there has been a change in the dominant species of the study plots after fire comparing the two surveys (IFN2 and IFN3) of the Spanish National Forest Inventory. This metric corresponds to a binary variable where 0 represents the maintenance of dominance and 1 represents a shift in species dominance after fire. We considered a species dominant when it was the main species and occupied 50% or more of the canopy cover in the surveyed IFN plot. We also assessed the difference in the percentage of the canopy cover of the pre-fire dominant species between IFN surveys (i.e., the capacity to recover the canopy after fire). This metric is positive if there is an increment of the canopy cover relative to the IFN2 and negative if there is a loss of canopy cover, which is expected after a wildfire, so negative values closer to zero indicate better recovery than highly negative values.

Climatic niche characterization

We characterized species' climatic niches according to their European distribution range using monthly climatic data obtained from CHELSA (ver 2.1 Karger *et al*., 2017, period 1979-2018). We extracted yearly climate values instead of the average values of the whole period to better characterize the inter-annual variability in environmental conditions experienced by the species (Perez-Navarro *et al* 2020). First, we extracted 12 of the bioclimate variables from all geographic locations in which the species were recorded in the high-resolution pan-European tree occurrence inventory (EUForest - Strona *et al*, 2016). We included 13121 occurrences for *P. halepensis*, 883779 occurrences for *Q. ilex* and 415428 occurrences for *P. nigra,* in which these species were respectively recorded as dominant. In the case of *P. halepensis*, the EU-level database overall should properly cover their environmental range within the study area, although the lack of records from North Africa can affect the characterization of the driest conditions,

Second, we characterized the climatic space occupied by each species using the combination of the 12 variables from CHELSA database, reducing the dimensionality of the 12 variables into multivariate axes using Principal Components Analysis (Broennimann *et al*. 2012, Figure 4.2). The composition of the axes that characterized the niche of each species is available in Supplementary Material Table SM4.1 and in Figure 4.2.

Then, the density of each species' occurrences within the respective climatic spaces was computed through kernel density estimates (i.e., the realized climatic niche, Broennimann *et al*., 2012). The species climatic optimum (also named niche centroid) was computed as the centre of mass of species density occurrence in the climatic space, i.e., the point representing the highest density of the occurrence of the species within the climatic niche. Also, the edge of the species' climatic distribution (i.e., niche edge) was calculated using the 95% density kernel. Outside this contour, the climatic conditions would be less suitable for the species, since only 5% of occurrences appear there. We selected several bioclimatic variables to interpret the climatic conditions that characterize the niche edge in its different contour sections.Accordingly, we defined a dry edge of the niche (Figure 4.2) characterized by high temperatures and high-temperature seasonality (positive contribution of Bio 1, 4, 5, 6, 10, 11 and 15), and a wet edge of the niche characterized by high precipitation (positive contribution of Bio 12, 13, 14, 16 and 17). Using the niche optimum as a relative centre, the projection (red shaded in Figure 4.2 A, C and E) of the bioclimatic variable 4 (temperature seasonality) and the bioclimatic variable 6 (mean daily minimum air temperature of the coldest month) on the contour of the niche edge were used to define the dry edge of the species' climatic niche (red contour in Figure 4.2 B, D and F). To define the wet edge of the species niche (blue contour in Figure 4.2 B, D and F) we used the projection of the bioclimate variable 14 (precipitation of the driest month) and the bioclimate variable 16 (precipitation of the wettest quarter) (blue shaded in Figure 4.2 A, C and E).

Finally, we projected within the species' climatic niche the coordinates of the selected National Forest Inventory plots of each species for the 5 years before the fire and for the years between fire occurrence and the IFN3 survey. For each of these points (i.e., population and year) we calculated the Euclidean distance to the niche optimum and to the closest point of the wet and the dry edges of the niche (Figure 4.2). Then, to standardize niche metrics among species due to their different niche areas, we weighted the distances (WD) to the niche centroid by the respective distance to the niche edge as $WD = DC * (DC + DE)^{-1}$ where DC and DE correspond to the distance to the centroid and the closest point of the edge, respectively. In this transformation, the distance to the niche edge is computed as positive if a point falls within the niche space and as negative when it falls outside of the niche space. So, points within the niche will have a weighted distance ≤1 and points outside the niche a weighted distance >1. We computed the mean distances and the standard deviation of the weighted distances to niche optimum and of the distances to both edges of the niche (wet and dry) for two periods, pre- and post-fire. In addition, we obtained the minimum distance to both wet and dry niche edges for the pre and post-fire periods.

R package ade4 (version 1.7-22, Dray & Dufour, 2007) were used to characterize the PCA. R packages ks (version 1.10.7, Chacón & Duong, 2018) and SDMTools (version 1.1-221, van der Wal *et al.*, 2014) were used to define the species' climatic niches and to compute distances to the niche optimum and edge.

Statistical analysis

Two generalized linear mixed models (GLMM) for each species were used to assess the relationship between the three species' regeneration after wildfires in relation to the position of their burned plots in niche space. In the models, the response variables were the change in the dominant species (i.e., species shift) and recovery of canopy cover. Predictor variables included the mean and standard deviation of the pre- and post-fire weighted distances to the centroid, as well as the mean, minimum and standard deviation of distances to the wet and dry edges. In all models, wildfire characteristics including severity and burned area were also included as predictor variables, and fire identity was considered as a random factor. Full models were then refined through backward selection and final models were selected based on the Akaike Information Criterion (AIC) and the explanation capacity (square R).

All statistical analyses were performed in R version 4.3.0 (Core Team, 2023).

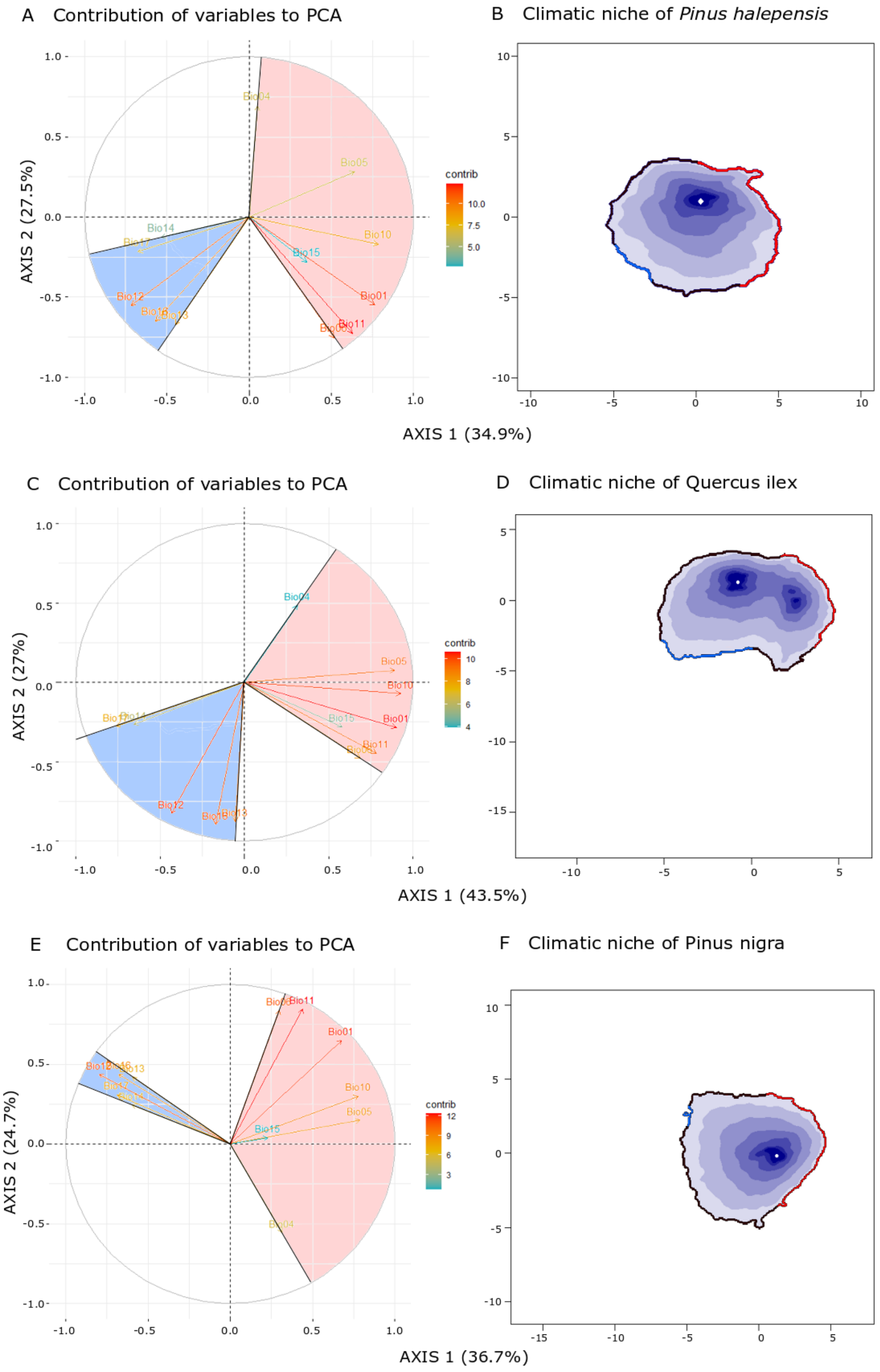


Figure 4.2. A, C and E: correlation circle obtained from the PCA performed with twelve selected bioclimatic variables describing the geographical locations in which *Pinus halepensis* (A), *Quercus ilex* (C) and *Pinus nigra* (E) have been recorded in the EUForest database (Mauri *et al.*, 2016b). Colour arrows indicate the contribution of each variable. Red shaded area indicates the arc that delineate the dry edge while blue shaded area indicates the equivalent for the wet edge. B, D and F: Environmental climate space (i.e., realized climatic niche) of *P. halepensis (B) Q. ilex* (D) and *P. nigra* (F) after translating the climatic variables of the geographical locations where species has been recorded to the environmental space defined by the PCA axes built for each species. In B, D and F, the white dot represents the niche optimum and the red and blue borders indicates the dry and wet edges of the niche, respectively.

4.3 Results

Both *P. halepensis* and *Q. ilex* remained as the dominant species in most of their burned plots (74.5% out of 644 burned plots, and 73.8% out of 107 burned plots, respectively, Supplementary material Figure SM4.1 and Tables SM4.2 and SM4.3), while *P. nigra* only remained as the dominant species in 22.5% out of its 225 burned plots (Supplementary material Figure SM4.1 and Table SM4.4). Also, where it regenerates, *P. nigra* have in general lower canopy recovery rates than *P. halepensis* and *Q. ilex*, although these two species showed higher intraspecific variability for this variable (Supplementary material Figure SM4.2).

In *P. halepensis* models, the species shift has a positive, significant relationship with the mean distance to the dry edge of the niche before fire (p-value<0.05, Figure 4.3, Supplementary material Table SM4.5), with the variability of the weighted distance to niche optimum after fire (p-value <0.05), with the mean distance to the dry edge after fire (p-value <0.05) and with the minimum distance to the wet edge after fire (p-value <0.05). It also has a negative, significant relationship with the minimum distance to the dry edge of the niche before fire (p-value <0.05), with the minimum distance to the dry edge after fire (p-value <0.05), with the variability of the distance to the dry edge after fire (p-value <0.05), and with the number of years between the fire and the plot inventory (p-value <0.01). The recovery of *P. halepensis* canopy cover between inventories was negatively related to the variability of the distance to the dry edge of the niche before fire (p-value <0.1, Figure 4.4, Supplementary material Table SM4.6), to the mean distance to the wet edge of the niche before fire (p-value <0.01) and to the mean weighted distance to centroid after fire (p-value <0.01). It also was positively related to the mean weighted distance to the niche optimum before fire (p-value <0.01), to the minimum distance to the wet edge before fire (p-value <0.01) and to the variability of distance to the wet edge before fire (p-value <0.01).

In *Q. ilex* models, the species shift showed a negative, significant relationship with the mean weighted distances to the niche optimum after fire (p-value <0.05, Figure 4.3, Supplementary material Table SM4.7), with the mean distance to the dry edge after fire (p-value <0.05), with the minimum distance to the wet edge after fire (p-value <0.001) and with the variability in the distances to the wet edge after fire (p-value <0.05). It had also a significant and positive relationship with the mean distance to the wet edge after fire (p-value <0.01) and with the severity of the fire (p-value<0.05). The recovery of *Q. ilex* canopy cover showed only a significant relationship with the mean weighted distance to the niche optimum after fire (p-value <0.01, Figure 4.4, Supplementary material Table SM4.8).

In *P. nigra* models, the species shift exhibited a positive relationship with mean distance to the wet edge after the fire (p-value <0.05, Figure 4.3, Supplementary material Table SM4.9), with the time since fire (i.e., years between fire and IFN3 inventory, p-value<0.05), and with fire severity (p-value<0.001); it also had a negative relationship with mean distance to the dry edge of the niche before the fire (p-value <0.1). There were no significant explanatory variables for the recovery of *P. nigra* canopy cover (Figure 4.4, Supplementary material Table SM4.10)

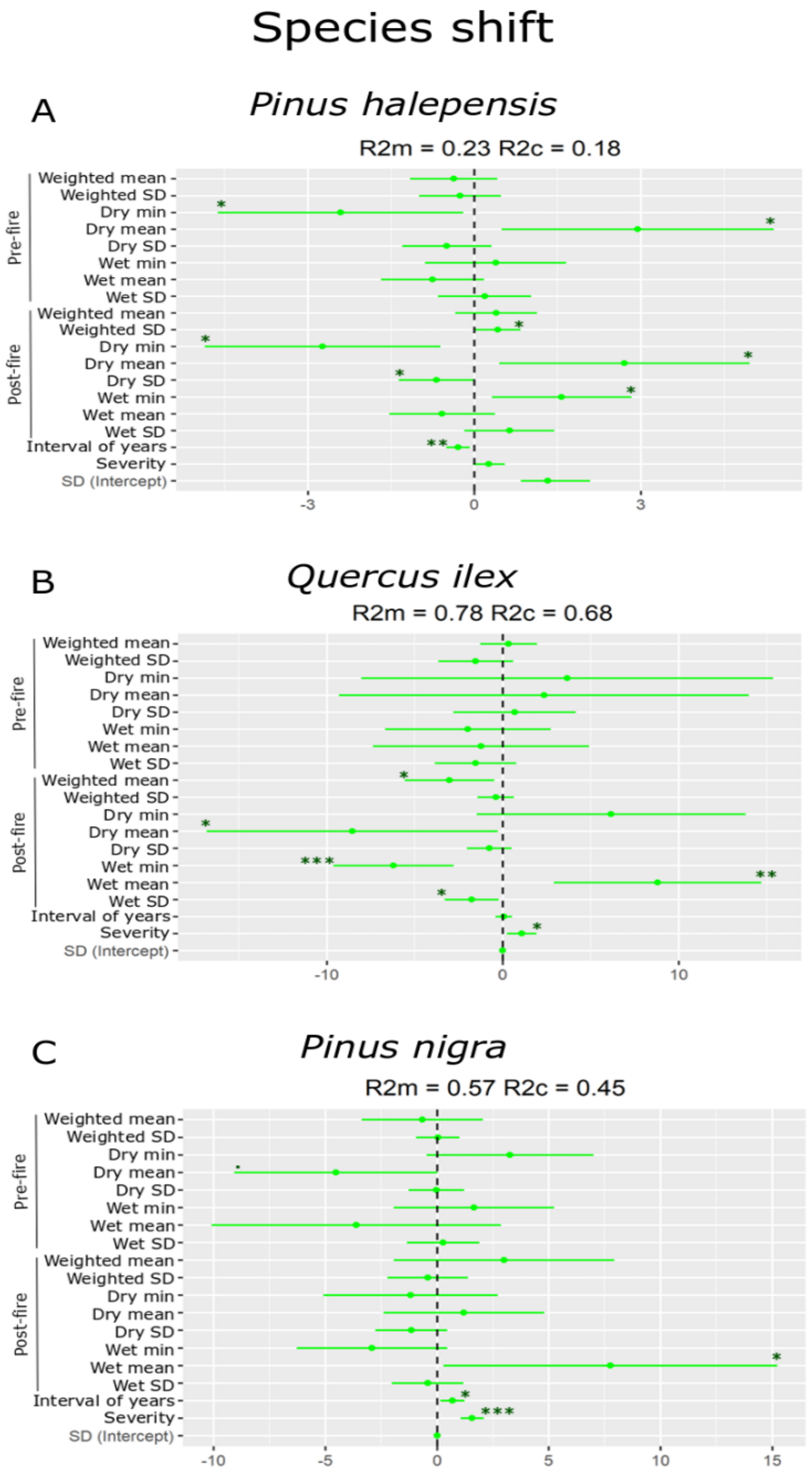


Figure 4.3: Results of the explanatory models for species shift after fire of the three species in relation to different niche metrics representing distances to the climatic niche optimum and the dry and wet edge of the niche, fire severity and time since wildfire (interval of years). See Table SM 4.11 for a full description of the variables' names. A) *Pinus halepensis*, B) *Quercus ilex*, C) *Pinus nigra*. R2m correspond to the Pseudo-R² (fixed effects) while R2c correspond to Pseudo-R² (total). A positive relationship indicates a higher probability of dominance loss. In all subplots, ***p-value <0.001, ** p-value < 0.01, * p-value < 0.05, · p-value < 0.1.

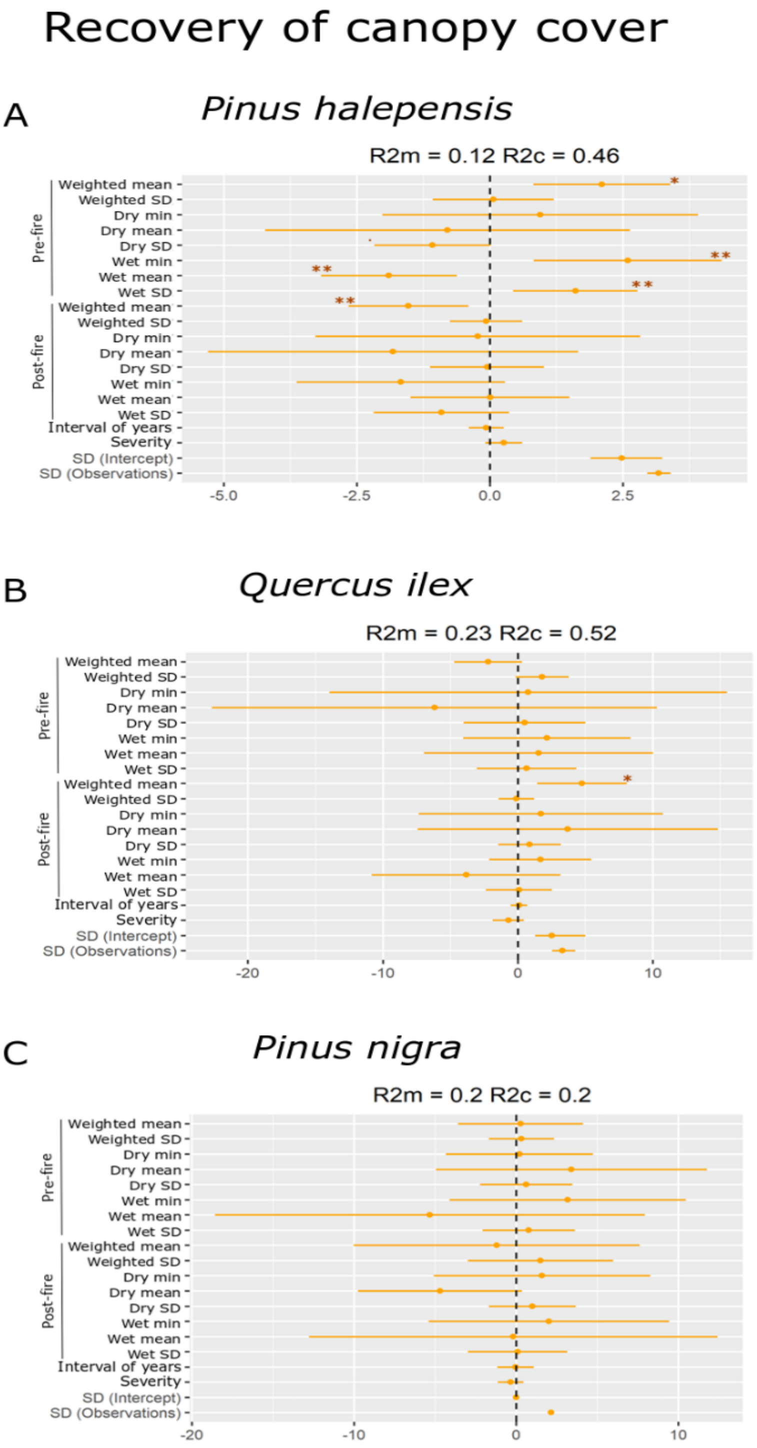


Figure 4.4: Results of the explanatory models for recovery of the canopy cover of the three species in relation to different niche metrics representing distances to the climatic niche optimum and the dry and wet edge of the niche,, fire severity and time since wildfire (interval of years). See Table SM 4.11 for a full description of the variables' names. A) *Pinus halepensis*, B) *Quercus ilex*, C) *Pinus nigra*. R2m correspond to the Pseudo-R^2 (fixed effects) while R2c correspond to Pseudo-R^2 (total). A positive relationship indicates a higher recovery of the canopy after fire. In all subplots, ***p-value <0.001, ** p-value < 0.01, * p-value < 0.05, · p-value < 0.1.

4.4 Discussion

Here we report the importance of populations' location within the species' realized climatic niche to understand the short-term resilience of Mediterranean tree species to wildfires, measured as the maintenance of species dominance and the recovery of the canopy cover after fire. *P. halepensis* appeared not only to be resilient to wildfires but it also performed better in drier conditions within its climatic niche, which could indicate greater resilience to drought as well (Zavala *et al.*, 2000). On the other hand, *Q. ilex* appeared to require post-fire humid conditions within its climatic niche to remain as the dominant species of the tree community. These resilience patterns were estimated from metrics informing about the species response in the short term. Although they are not necessarily representative of the trajectories of the burned populations in the long term, they are indicative of the initial response of burned areas that will, therefore, condition the long-term dynamics of the sites.

Our results also corroborate the importance of regenerative traits for post-fire resilience (Enright *et al.*, 2014). The results showed higher resilience in terms of post-fire maintenance of tree species dominance in species exhibiting post-fire regenerative strategies, by resprouting from underground and epicormic buds in the case of *Q. ilex*, or by the establishment of new plants from seeds released by serotinous pinecones in the case of *P. halepensis* (Clarke *et al.*, 2013; Núñez & Calvo, 2000). The efficiency of these mechanisms resulted in the permanence after the wildfire of these fire-adapted species as dominant in around 75% of burned plots. In contrast, *P. nigra* burned plots suffered more frequently (ca. 80%) a shift of the pre-fire dominant species, thus emphasizing that it is a species barely resilient to wildfires (Ordóñez *et al.*, 2005).

Fire severity appeared as a significant variable in explaining the shift of dominant species in the case of *P. nigra* and *Q. ilex*, but not in *P. halepensis*. This supports the notion that Aleppo pine is well adapted to stand replacing wildfires, even when they destroy standing trees (Parra & Moreno, 2018). Yet, the success of *P. halepensis* post-fire establishment has been reported to be dependent on other variables, such as post-fire climate (in our cases corresponding to the position of burned populations within the climatic niche), the size and the viability of the seed bank, the predation of the seeds, or the site topography, among others (Broncano *et al.*, 2007; Elvira *et al.*, 2021; Pausas & Keeley, 2014). Although communities dominated by seeder species may show heavy impact on their structure under highly intense wildfires, compared with communities dominated by resprouters (Jimeno-Llorente *et al*., 2023), the establishment of cohorts of seeder trees, such as *P. halepensis*, may allow maintaining their dominance in the mid-term regardless of the severity of the wildfires.

However, *P. halepensis* showed lower resilience (i.e., higher replacement by other species) in sites where pre-fire climatic conditions were far to the dry limit of the climatic niche (i.e., higher mean distance to the dry edge of the niche). Therefore, although pre-fire conditions could be close to the niche optimum in these sites, our assessment reveals that more humid conditions before the fire actually promoted the shift to other species, such as *Q. ilex* or *Arbutus unedo,* that correspond to a more advanced successional stage (Pausas, *et al*., 2004a, Supplementary material Table SM4.2). In contrast, the locations closer to the dry edge of the niche of *P. halepensis* may be also suboptimal for other potentially replacing species, favouring Aleppo pine resilience in these locations. In addition, in semi-arid locations, *P. halepensis* makes an important reproductive effort by increasing the production of serotinous pinecones (Alfaro-Sánchez *et al*., 2015) which may ensure the seed bank after the fire and improve the maintenance of *P. halepensis* dominance. However, the existence of extremely dry years before the fire (i.e., minimum distances to the dry edge of the niche) may have favoured the opening of serotinous cones before the fire (Espelta *et al*., 2011), reducing seed availability and, consequently, of recruiting pines after fire. In fact, extremely dry years were associated to shifts to other species such as *Juniperus oxycedrus*, which may find their optimal distribution in drier conditions than Aleppo pine (Supplementary material Table SM4.2).

The presence of dry, post-fire conditions on average (i.e., smaller mean distances to the dry edge of the niche) was also relevant in promoting Aleppo pine maintenance as the dominant species in the plots. As *P. halepensis* is one of the most thermophilic and xerophilic tree species in the Iberian Peninsula (Rouget *et al*., 2001), dry conditions for this species are likely to be also very unfavourable for other species, thus giving a competitive advantage to Aleppo pine recruits (Zavala *et al*., 2000). This is consistent with the result showing that great variability in the distance to the dry edge of the niche during the post-fire years reduced the probability of loss of Aleppo pine dominance, likely because this high climatic variability would imply adverse conditions (i.e., drought-related conditions) affecting more the potential replacing species than to *P. halepensis*, (Zavala *et al*., 2000). On the other hand, although seedling mortality may leave more resources for *P. halepensis* survivors (Chapter 3, Turrión *et al*., 2022), under extremely dry conditions after fire (i.e., post-fire year close to the dry edge of the niche) the recruits density would not be high enough to maintain the species' dominance, thus leading to a loss of resilience and a shift in dominant species (Elvira *et al*., 2021). Alternatively, the presence of extremely wet conditions during the first years after fire promoted the maintenance of *P. halepensis* as the dominant species, highlighting the sensitivity of seedlings to water availability (Elvira *et al.*, 2021). A year with high rainfall can determine important growth rates, determining stem size (height, diameter), and reserves accumulation in young plants (Royo *et al*., 2001).

The recovery of canopy cover in *P. halepensis* burned forests was also favoured in populations where conditions were distant from the niche optimum but closer to the wet edge of the niche during pre-fire years. This may be due to more successful canopy recovery of surviving trees which stored abundant reserves during suboptimal wet pre-fire years (Santini *et al*., 2019). However, years with minimum distance to the wet edge of the *P. halepensis*' niche impose difficulties in recovering its canopy cover after fire, probably because, under such wet conditions, other species (e.g., *Quercus* spp.) may be more competitive, reducing the ability of *P. halepensis* to colonize and to grow after fire. We also observed that sites with high variability in the pre-fire distances to the dry edge of the niche exhibited lower recovery of the canopy cover, while greater variability in the distance to the wet edge increases the recovery of the canopy cover. As stated above, greater variability under suboptimal dry conditions could promote a shift in the resource allocation of Aleppo pine from growth to reproduction (Alfaro-Sánchez *et al*., 2015) whereas high variability in relation to the wet edge represents humid conditions that create larger canopies that might remain after fire. Finally, near-optimal conditions after the fire (i.e., closer to the niche optimum) also favour canopy development. This pattern agrees with results reported in Chapter 3, where larger mean distances to the dry edge of the niche were associated with higher recruits of Aleppo pines. Recruits may be very sensitive to favourable conditions that could thus promote faster growth and species cover (Royo *et al*., 2001).

Although they are not completely comparable, the post-fire species shift and canopy cover models provide, overall, insights into the resilience capacity of Aleppo pine throughout its climatic niche. The species shift model suggests that populations in the driest portion of the niche would experience a trade-off in the allocation of resources between growth and seed production, which could derive in a greater production of the resistance structures (serotinous cones) that allow the species to remain after the wildfire (Alfaro-Sánchez *et al*., 2015; Zavala *et al*., 2000). However, in populations in optimal and humid suboptimal areas, resources may be mostly allocated to canopy growth (Gonzalez *et al*., 2023) and reserves storage (Santini *et al*., 2019) respectively. Finally, when very close to its wettest niche edge, *P. halepensis* populations would be prone to be replaced by other species which are more competitive under these conditions.

In the case of *Q. ilex*, populations exhibiting post-fire years far from the wet edge of the niche (both near the optimum and the dry edge of the niche) were more prone to a shift of the dominant species, likely due to reduction of the growth of *Q. ilex* resprouts. Wetter environments result in a higher amount of resources for resprout growth, consistent with the observed higher assimilation rates of resprouts with soil humidity elsewhere (Bussotti & Pollastrini, 2020; Pollastrini *et al*., 2019). However, particularly humid years after fire (i.e., small minimum distances to the wet edge of the niche) can also favour species shift, likely due to a better recovery and growth of potentially replacing species such as *Arbutus unedo* or *Quercus suber* (Supplementary material Table SM4.3). Locations with greater variability in the distance to the wet edge of the niche after the wildfire exhibited higher maintenance of *Q. ilex*, probably because this species has important reserve organs that buffer environmental variability (El Omari *et al*., 2003). In locations with post-fire conditions more distant from the niche optimum, the growth of the *Q. ilex* canopy cover appears enhanced. This may be partially explained because greater distances to the centroid can represent closer distances to the wet edge of the niche, and by the presence of two centres of high density of occurrences within the Holm oak niche (Figure 4.2). Finally, greater severity of wildfires was associated with species shift in burned Holm oak populations, likely because high-intensity wildfires damage the bud bank, or result in resprouts more sensitive to dry conditions than following low-intensity wildfires (Parra & Moreno, 2018). However, we failed to find a significant relationship between fire severity and canopy recovery, partially because resprouts would not have been large enough to be sampled in IFN3.

For *P. nigra*, locations with mean pre-fire conditions far from the niche optimum (i.e., far from the species' optimal climate) were more likely to undergo a shift in species dominance after the fire, likely because under these conditions growth rates were low, eventually reducing resources and structures allowing survival, relative to other co-occurring species with more effective post-fire regenerative strategies (i.e., resprouting *Quercus* spp.). The occurrence of post-fire years with climate conditions falling near the wet edge of the niche promoted in some cases the maintenance of *P. nigra* as dominant, probably due to a growth enhancement of the surviving trees. Plots dominated by *P. nigra* before fire showed a greater shift of the dominant species with increasing time lapse between the fire and the post-fire IFN3 survey probably because despite the existence of survivors (Ordóñez *et al*., 2005) delayed mortality eventually occurs. Also, enhanced growth of other species better adapted to the passage of fire or to post-fire conditions would favour their establishment and growth, eventually leading to species replacement (Enright *et al*., 2014). Finally, as expected in a fire-sensitive species, greater fire severity translates into important shifts in the dominance of black pine, because the high fire-induced mortality of adults is not balanced by the establishment of new seedlings, as no seed sources remain.

Overall, this study shows that the climatic niche of the species constitutes a useful framework for understanding short-term resilience capacity to a major disturbance such as fire. It also expands the knowledge acquired on the relationship of demographic post-fire responses of *P. halepensis* in relation to the populations' position within the species' niche (Elvira *et al*., 2021, Chapter 3). The characterization of the realized climatic niche has been used also for other forest and shrubland species that have suffered disturbances such as drought or bark beetle attacks (Díaz-Borrego *et al*., 2024; Jaime *et al*., 2019, 2022; Margalef-Marrase *et al*., 2020, 2022; Pérez Navarro *et al*., 2019). Also, the differentiation of the humid and dry limits of the niche provides relevant information to interpret the role of population position in niche space (Chapter 3). The differential post-fire response of the three studied species according to the location of their populations within the species' climatic niche can also reveal their differential sensitivity to the new conditions expected under climate change. Although both *P. halepensis* and *Q. ilex* are considered to be well adapted to fires in the Mediterranean region (Díaz-Delgado *et al*., 2002), extreme drought conditions into the future may challenge more post-fire regeneration of *Q. ilex* (Barbeta *et al*., 2013) than of *P. halepensis*. Therefore, contextualizing this finding in future climate change scenarios, where wildfires, droughts and heat waves will be increasingly more intense and frequent (IPCC, 2023), sudden ecosystems shifts are likely to occur (Batllori *et al*., 2019). In this scenario, *P. halepensis* appears better suited than *Q. ilex* to these new compound fire and drought regimes in the Iberian Peninsula. Current and future conditions produced by climate change can displace populations from their historical location in the niche and even take them outside of it, so the construction of the niches can be a tool to understand the magnitude of the climate change effects on vegetation. Additionally, regeneration behaviour could differ from the species' historical pattern due to the acclimation to new fire regimes (Pausas & Keeley, 2014). On the other hand, emerging fire regimes can alter the effectiveness of reproductive and regenerative strategies, creating opportunities for colonization by other species. Finally, better characterization of the realized climatic niche of seedlings and saplings, which may differ from the adult niche (Carscadden *et al*., 2020; de Luis *et al*., 2009), would allow increasing our understanding of niche metrics to infer ecosystem resilience into the future. These caveats highlight new research topics to work on in the future.

4.5 Conclusions

The short-term resilience of tree populations in front of wildfires, characterized as the maintenance of species' dominance in the community, is determined by the presence of a fire-prone regeneration strategy. However, resilience is also modulated by the position of the burned populations within the realized species' climatic niche, especially the distance to the wet and dry edges of the niche. In the case of *P, halepensis*, the occurrence of mild drought-related conditions before and after fire enhances the maintenance of its dominance while the presence of extremely dry years promotes the loss of it. Additionally, the occurrence of wetter suboptimal conditions enhances the recovery of the canopy cover in this species. For *Q. ilex*, community dominance is maintained when wet conditions occur after the fire, although the presence of extremely wet years favours species shift after burning. The resilience of *P. nigra* is negatively associated with high-severity fires regardless of pre- and post-fire climate conditions. Overall, under future scenarios of climatic change where more frequent and intense droughts are expected, *P. halepensis* may be the most resilient species to the new disturbance regimens.

Supplementary material

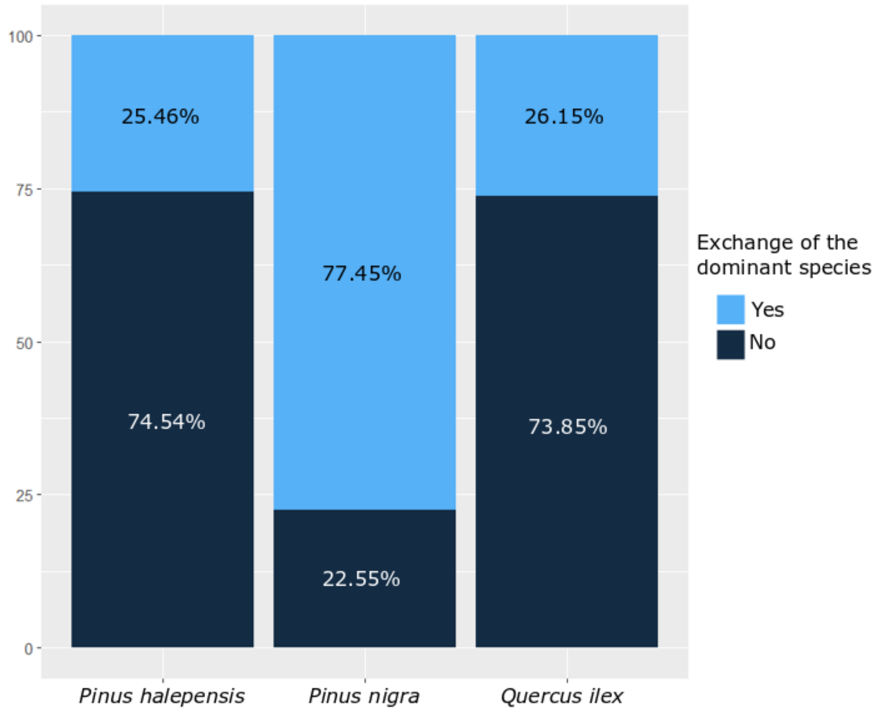


Figure SM4.1: Data distribution of the binomial variable species shift, for each of the three species

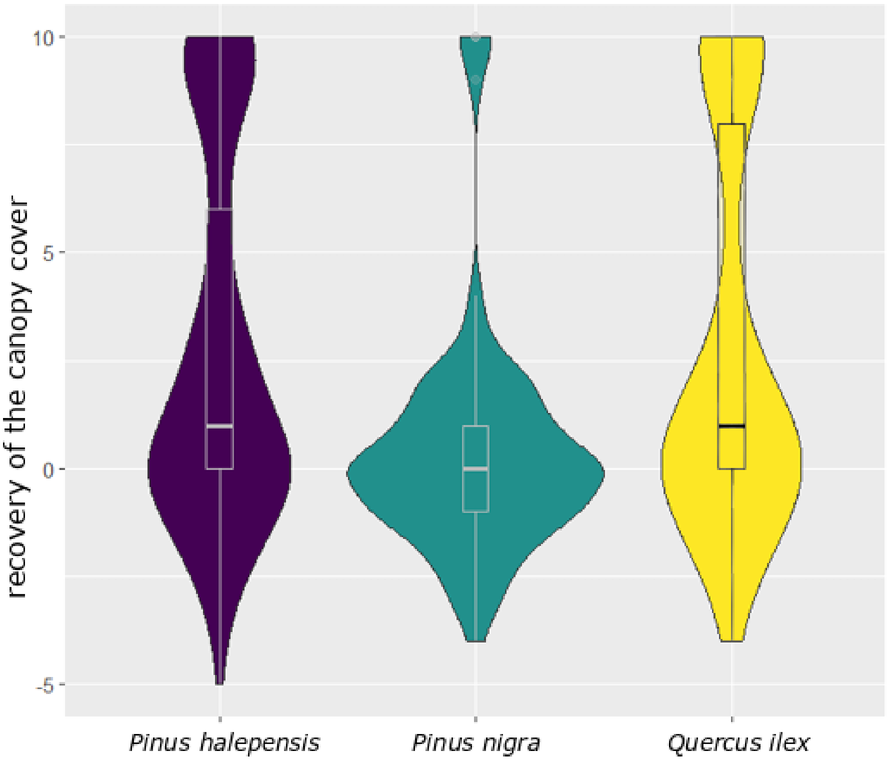


Figure SM4.2: Data distribution of the percentage of canopy cover recovery for the three studied species

Table SM4.1: Bioclimate variables that compose the axes that characterized the niche of each species.

For *P. halepensis*, the first axis was positively related to the annual mean temperature (Bio1), the mean temperature of the warmest quarter (Bio10) and the annual precipitation (Bio12); and negatively related to the maximum temperature of the warmest month (Bio5) and the precipitation of driest quarter (Bio17). The second axis was positively related to the minimum temperature of the coldest month (Bio6) and negatively related to the mean temperature of the coldest quarter (Bio11), the precipitation of the wettest quarter (Bio16) and the precipitation of the wettest month (Bio13).
For *Q. ilex*, the first axis was positively related to the mean temperature of the warmest quarter (Bio10), the annual mean temperature (Bio1), the maximum temperature of the warmest month (Bio5), the mean temperature of the coldest quarter (Bio11) and the minimum temperature of the coldest month (Bio6); and negatively related to the precipitation of driest quarter (Bio17) and precipitation of the driest month (Bio14). The second axis was negatively related to, the precipitation of the wettest quarter (Bio16), the precipitation of the wettest month (Bio13) and the annual precipitation (Bio12).
For *P. nigra*, the first axis was positively related to the maximum temperature of the warmest month (Bio5), the mean temperature of the warmest quarter (Bio10) and the annual mean temperature (Bio1); and negatively related to the annual precipitation (Bio12), the precipitation of driest quarter (Bio17) and the precipitation of the wettest quarter (Bio16). The second axis was positively related to the minimum temperature of the coldest month (Bio6), the mean temperature of the coldest quarter (Bio11) and the annual mean temperature (Bio1).

Table SM4.2: Species shift in IFN3 in plots with *Pinus halepensis* in IFN2

CODE_SP	NUMBER OF PLOTS	PROPORTION	SPECIES
4	2	0.00298	*Rhamnus alaternus*
8	1	0.00149	*Phillyrea latifolia*
23	1	0.00149	*Pinus pinea*
24	491	0.73393	*Pinus halepensis*
25	6	0.00896	*Pinus nigra*
26	2	0.00298	*Pinus pinaster*
42	1	0.00149	*Quercus petraea*
44	6	0.00896	*Quercus faginea*
45	58	0.08669	*Quercus ilex ssp. ballota*
56	1	0.00149	*Ulmus minor*
58	1	0.00149	*Populus nigra*
66	5	0.00747	*Olea europaea*
68	18	0.02690	*Arbutus unedo*
69	1	0.00149	*Phoenix spp.*
74	1	0.00149	*Corylus avellana*
75	1	0.00149	*Juglans regia*
95	1	0.00149	*Prunus spp.*
237	29	0.04334	*Juniperus oxycedrus*
243	14	0.02092	*Quercus pubescens*
291	1	0.00149	Other species
369	5	0.00747	Other species

Table SM4.3: Species shift in IFN3 in plots with *Quercus ilex* in IFN2

CODE_SP	NUMBER OF PLOTS	PROPORTION	SPECIES
6	1	0.00775	*Myrtus communis*
16	1	0.00775	*Pyrus spp.*
24	5	0.03875	*Pinus halepensis*
25	2	0.01550	*Pinus nigra*
26	1	0.00775	*Pinus pinaster*
28	1	0.00775	*Pinus radiata*
42	1	0.00775	*Quercus petraea*
44	4	0.03100	*Quercus faginea*
45	95	0.73643	*Quercus ilex ssp. ballota*
46	5	0.03875	*Quercus suber*
66	2	0.01550	*Olea europaea*
68	1	0.00775	*Arbutus unedo*
92	1	0.00775	*Robinia pseudoacacia*
237	2	0.01550	*Juniperus oxycedrus*
243	1	0.00775	*Quercus pubescens*
369	1	0.00775	Other species

Table SM4.4: Species shift in IFN3 in plots with *Pinus nigra* in IFN2

CODE_SP	NUMBER OF PLOTS	PROPORTION	SPECIES
2	2	0.00581	Other species
21	1	0.00290	*Pinus sylvestris*
23	2	0.00581	*Pinus pinea*
24	21	0.06104	*Pinus halepensis*
25	82	0.23837	*Pinus nigra*
26	2	0.00581	*Pinus pinaster*
42	1	0.00290	*Quercus petraea*
44	48	0.13953	*Quercus faginea*
45	46	0.13372	*Quercus ilex ssp. ballota*
68	3	0.00872	*Arbutus unedo*
91	2	0.00581	*Buxus sempervirens*
237	7	0.02034	*Juniperus oxycedrus*
243	112	0.32558	*Quercus pubescens*
295	1	0.00290	Other species

Table SM4.5: Model of *Pinus halepensis* for changes in the dominant species considering all variables (except for Fire severity and Years between fire and inventory, the variables correspond to distances in the species' climatic niche): AIC = 615.61, BIC = 704.96, Pseudo-R² (fixed effects) = 0.227, Pseudo-R² (total) = 0.496. CI corresponds to the Confidence Interval.

	PREDICTORS	ODDS RATIOS	CI	P
	(INTERCEPT)	3.45	0.58 – 20.43	0.173
PRE-FIRE DISTANCES	WEIGHTED MEAN	0.69	0.31 – 1.52	0.356
	WEIGHTED SD	0.77	0.37 – 1.61	0.489
	DRY EDGE MIN	0.09	0.01 – 0.82	**0.033**
	DRY EDGE MEAN	18.89	1.63 – 218.61	**0.019**
	DRY EDGE SD	0.61	0.27 – 1.36	0.224
	WET EDGE MIN	1.47	0.41 – 5.23	0.554
	WET EDGE MEAN	0.47	0.19 – 1.19	0.110
	WET EDGE SD	1.20	0.52 – 2.78	0.665
POST- FIRE DISTANCES	WEIGHTED MEAN	1.48	0.71 – 3.08	0.296
	WEIGHTED SD	1.52	1.00 – 2.30	**0.048**
	DRY EDGE MIN	0.06	0.01 – 0.54	**0.012**
	DRY EDGE MEAN	14.91	1.56 – 142.34	**0.019**
	DRY EDGE SD	0.51	0.26 – 1.00	**0.049**
	WET EDGE MIN	4.81	1.37 – 16.89	**0.014**
	WET EDGE MEAN	0.56	0.22 – 1.45	0.230
	WET EDGE SD	1.88	0.84 – 4.24	0.126
	INTERVAL OF YEARS	0.74	0.60 – 0.92	**0.006**
	FIRE SEVERITY	1.30	0.97 – 1.73	0.076

Table SM4.6: Model of *Pinus halepensis* for recovery of canopy cover considering all variables (except for Fire severity and Years between fire and inventory, the variables correspond to distances in the species' climatic niche): AIC = 2645.72, BIC = 2733.89, Pseudo-R^2 (fixed effects) = 0.123, Pseudo-R^2 (total) = 0.455. CI corresponds to the Confidence Interval.

	PREDICTORS	*ESTIMATES*	*CI*	*P*
	(INTERCEPT)	2.82	-0.17 – 5.80	0.064
PRE-FIRE DISTANCES	WEIGHTED MEAN	2.10	0.81 – 3.39	**0.001**
	WEIGHTED SD	0.06	-1.07 – 1.20	0.911
	DRY EDGE MIN	0.94	-2.02 – 3.91	0.532
	DRY EDGE MEAN	-0.80	-4.23 – 2.63	0.648
	DRY EDGE SD	-1.08	-2.17 – 0.01	*0.052*
	WET EDGE MIN	2.59	0.82 – 4.35	**0.004**
	WET EDGE MEAN	-1.90	-3.17 – -0.63	**0.004**
	WET EDGE SD	1.61	0.44 – 2.78	**0.007**
POST- FIRE DISTANCES	WEIGHTED MEAN	-1.53	-2.66 – -0.41	**0.008**
	WEIGHTED SD	-0.07	-0.75 – 0.61	0.834
	DRY EDGE MIN	-0.23	-3.28 – 2.82	0.883
	DRY EDGE MEAN	-1.82	-5.30 – 1.66	0.304
	DRY EDGE SD	-0.05	-1.13 – 1.02	0.921
	WET EDGE MIN	-1.68	-3.63 – 0.28	0.092
	WET EDGE MEAN	0.00	-1.49 – 1.50	0.996
	WET EDGE SD	-0.91	-2.18 – 0.36	0.158
	INTERVAL OF YEARS	-0.07	-0.40 – 0.26	0.667
	FIRE SEVERITY	0.26	-0.09 – 0.60	0.143

Table SM4.7: Model of *Quercus ilex* for changes in the dominant species considering all variables (except for Fire severity and Years between fire and inventory, the variables correspond to distances in the species' climatic niche): AIC = 115.96, BIC = 169.42, Pseudo-R^2 (fixed effects) = 0.781, Pseudo-R^2 (total) = 0.78. CI corresponds to the Confidence Interval.

	PREDICTORS	ODDS RATIOS	CI	P
	(INTERCEPT)	0.11	0.00 – 4.58	0.248
PRE-FIRE DISTANCES	WEIGHTED MEAN	1.40	0.28 – 7.00	0.683
	WEIGHTED SD	0.22	0.03 – 1.80	0.157
	DRY EDGE MIN	38.67	0.00 – 4639450.02	0.540
	DRY EDGE MEAN	10.39	0.00 – 1193666.49	0.694
	DRY EDGE SD	1.97	0.06 – 63.94	0.702
	WET EDGE MIN	0.14	0.00 – 15.21	0.409
	WET EDGE MEAN	0.29	0.00 – 134.11	0.693
	WET EDGE SD	0.21	0.02 – 2.15	0.190
POST- FIRE DISTANCES	WEIGHTED MEAN	0.05	0.00 – 0.62	**0.020**
	WEIGHTED SD	0.68	0.24 – 1.90	0.459
	DRY EDGE MIN	475.36	0.23 – 981457.98	0.113
	DRY EDGE MEAN	0.00	0.00 – 0.76	**0.043**
	DRY EDGE SD	0.46	0.13 – 1.65	0.235
	WET EDGE MIN	0.00	0.00 – 0.06	**<0.001**
	WET EDGE MEAN	6577.04	18.12 – 2386833.35	**0.003**
	WET EDGE SD	0.17	0.04 – 0.80	**0.025**
	INTERVAL OF YEARS	1.06	0.66 – 1.69	0.815
	FIRE SEVERITY	2.95	1.27 – 6.89	**0.012**

Table SM4.8: Model of *Quercus ilex* for recovery of canopy cover considering all variables (except for Fire severity and Years between fire and inventory, the variables correspond to distances in the species' climatic niche): AIC = 410.65, BIC = 459.59, Pseudo-R² (fixed effects) = 0.229, Pseudo-R² (total) = 0.516. CI corresponds to the Confidence Interval.

	PREDICTORS	ESTIMATES	CI	P
	(INTERCEPT)	0.44	-4.48 – 5.36	0.858
PRE-FIRE DISTANCES	WEIGHTED MEAN	-2.20	-4.71 – 0.32	0.086
	WEIGHTED SD	1.80	-0.16 – 3.76	0.070
	DRY EDGE MIN	0.77	-13.94 – 15.48	0.917
	DRY EDGE MEAN	-6.18	-22.67 – 10.31	0.456
	DRY EDGE SD	0.49	-4.01 – 5.00	0.827
	WET EDGE MIN	2.15	-4.05 – 8.36	0.490
	WET EDGE MEAN	1.53	-6.95 – 10.02	0.719
	WET EDGE SD	0.64	-3.04 – 4.33	0.728
POST- FIRE DISTANCES	WEIGHTED MEAN	4.75	1.43 – 8.08	**0.006**
	WEIGHTED SD	-0.12	-1.43 – 1.20	0.859
	DRY EDGE MIN	1.70	-7.35 – 10.76	0.707
	DRY EDGE MEAN	3.70	-7.43 – 14.82	0.508
	DRY EDGE SD	0.87	-1.45 – 3.19	0.456
	WET EDGE MIN	1.67	-2.12 – 5.45	0.381
	WET EDGE MEAN	-3.84	-10.83 – 3.16	0.277
	WET EDGE SD	0.08	-2.36 – 2.52	0.948
	INTERVAL OF YEARS	0.09	-0.54 – 0.71	0.779
	FIRE SEVERITY	-0.71	-1.87 – 0.46	0.230

Table SM4.9: Model of *Pinus nigra* for changes in the dominant species considering all variables (except for Fire severity and Years between fire and inventory, the variables correspond to distances in the species' climatic niche): AIC = 198.67, BIC = 266.99, Pseudo-R² (fixed effects) = 0.570, Pseudo-R² (total) = 0.570. CI corresponds to the Confidence Interval.

	PREDICTORS	ODDS RATIOS	CI	P
	(INTERCEPT)	0.08	0.00 – 1.41	0.083
PRE-FIRE DISTANCES	WEIGHTED MEAN	0.52	0.03 – 7.83	0.636
	WEIGHTED SD	1.04	0.39 – 2.74	0.943
	DRY EDGE MIN	26.24	0.63 – 1092.45	0.086
	DRY EDGE MEAN	0.01	0.00 – 1.03	*0.052*
	DRY EDGE SD	0.97	0.28 – 3.36	0.964
	WET EDGE MIN	5.19	0.14 – 187.47	0.368
	WET EDGE MEAN	0.03	0.00 – 17.40	0.273
	WET EDGE SD	1.32	0.26 – 6.64	0.739
POST- FIRE DISTANCES	WEIGHTED MEAN	19.87	0.14 – 2760.19	0.235
	WEIGHTED SD	0.66	0.11 – 4.00	0.653
	DRY EDGE MIN	0.31	0.01 – 15.24	0.554
	DRY EDGE MEAN	3.32	0.09 – 120.81	0.512
	DRY EDGE SD	0.32	0.06 – 1.58	0.160
	WET EDGE MIN	0.05	0.00 – 1.58	0.090
	WET EDGE MEAN	2325.09	1.33 – 4064821.46	**0.042**
	WET EDGE SD	0.66	0.13 – 3.27	0.607
	INTERVAL OF YEARS	1.99	1.16 – 3.42	**0.013**
	FIRE SEVERITY	4.80	2.86 – 8.05	**<0.001**

Table SM4.10: Model of *Pinus nigra* for recovery of canopy cover considering all variables (except for Fire severity and Years between fire and inventory, the variables correspond to distances in the species' climatic niche): AIC = 230.49, BIC = 272.26, Pseudo-R^2 (fixed effects) = 0.190, Pseudo-R^2 (total) = 0.20. CI corresponds to the Confidence Interval.

	PREDICTORS	ESTIMATES	CI	P
	(INTERCEPT)	1.34	-4.13 – 6.81	0.621
PRE-FIRE DISTANCES	WEIGHTED MEAN	0.27	-3.59 – 4.13	0.888
	WEIGHTED SD	0.32	-1.69 – 2.33	0.749
	DRY EDGE MIN	0.19	-4.34 – 4.73	0.931
	DRY EDGE MEAN	3.40	-4.96 – 11.76	0.414
	DRY EDGE SD	0.61	-2.23 – 3.45	0.665
	WET EDGE MIN	3.17	-4.12 – 10.47	0.383
	WET EDGE MEAN	-5.33	-18.59 – 7.93	0.419
	WET EDGE SD	0.77	-2.08 – 3.62	0.585
POST- FIRE DISTANCES	WEIGHTED MEAN	-1.21	-10.03 – 7.61	0.782
	WEIGHTED SD	1.49	-2.99 – 5.97	0.503
	DRY EDGE MIN	1.58	-5.10 – 8.27	0.633
	DRY EDGE MEAN	-4.70	-9.75 – 0.34	0.067
	DRY EDGE SD	0.99	-1.68 – 3.66	0.457
	WET EDGE MIN	2.01	-5.41 – 9.43	0.585
	WET EDGE MEAN	-0.18	-12.77 – 12.41	0.977
	WET EDGE SD	0.08	-2.98 – 3.14	0.956
	INTERVAL OF YEARS	-0.05	-1.16 – 1.07	0.935
	FIRE SEVERITY	-0.35	-1.13 – 0.44	0.375

Table SM4.11: Explanation of the variables' names used in the figures

WEIGHTED MEAN	Mean weighted distance to the niche optimum
WEIGHTED SD	Standard Deviation of the weighted distances to the niche optimum
DRY MIN	Minimum distance to the dry edge of the niche
DRY MEAN	Mean distance to the dry edge of the niche
DRY SD	Standard Deviation of the distances to the dry edge of the niche
WET MIN	Minimum distance to the wet edge of the niche
WET MEAN	Mean distance to the wet edge of the niche
WET SD	Standard Deviation of the distances to the wet edge of the niche

Chapter 5

General discussion

The regeneration responses to fire regimes and, specifically the resilience capacity of major Mediterranean tree species at different spatiotemporal scales, combined with the effects of drought-related conditions, are complex. The regeneration of the populations implies multiple processes (see Chapter 1, Figure 1.1) that extend over time (e.g., germination and establishment are conditioned by the production of a seed bank during the years before fire) and involves medium and long-term biotic interactions. This obligates us to examine different scales, from macroclimatic conditions to microsite characteristics. Furthermore, the influence of fire-drought compound disturbance regimes under the climate change context is expected to increase in the Mediterranean Basin as a result of intensified frequency and intensity of hotter and drier conditions (IPCC, 2023). This could alter the tree species' resilience to fire events (Batllori *et al*., 2017, 2019; Baudena *et al*., 2020). In this PhD Thesis, I have investigated the effects of pre- and post-fire climatic conditions related to drought on the resilience of different Mediterranean tree species from tree level to regional scale, under the conceptual framework of the species' realized climatic niche. My work increases the existing knowledge on “Why do some tree populations regenerate vigorously after being burned while others perish and are substituted by other species?”. Throughout the different studies constituting this PhD Thesis, I have used the environmental position of the tree populations within the realized species' climatic niche, together with fire properties and microsite conditions of regeneration, to assess ecosystem resilience. The realized climatic niche framework allows the inclusion of the historical climatic conditions that affect the species' populations, which has proved useful for understanding demographic processes that extend over time or that are conditioned by the history of the population.

5.1 Niche position and resilience

Niche position metrics derived from the realized species' climatic niche can explain the recovery dynamics after fire in Mediterranean forest tree species. I examined the importance of these metrics for *Pinus halepensis* post-fire response in north-east Spain (Chapters 2 and 3) and for three forest species with contrasted regeneration traits across Spain (*Pinus halepensis*, a seeder species; *Quercus ilex*, a resprouter species; *Pinus nigra*, a fire sensitive species; Chapter 4). In these studies, I found that the historical climatic conditions, translated into the species' climatic niche encompassing interannual variability, influence the resilience capacity of tree populations and recruits' performance to fire. Specifically, I found that the distance to niche optimum and niche edge of burned populations both before and after fire (Chapters 2 and 4), have a relevant role in explaining species’ response to fire events. These results reinforce the findings of previous research approaches describing a relationship between the position in the species' realized climatic niche and shrubland and forest ecosystems' response to disturbances, including extreme drought and bark beetle attack (e.g., Díaz-Borrego *et al*., 2024; Jaime *et al*., 2019, 2022; Lloret & Kitzberger, 2018; Margalef-Marrase *et al*., 2020; Pérez Navarro *et al*., 2019). However, this PhD Thesis is pioneer in providing empirical evidence of the suitability of niche position metrics to evaluate ecosystem response in front of compound fire-drought regimes. Importantly, my work represents the first approach in assessing the influence of changes within the niche space, also reflecting the specific climate conditions that characterize the dry and wet climatic niche edges. In addition, and due to the increased relevance of drought conditions in the climatic change context, I have particularly evaluated drought gradients across this PhD Thesis (i.e., low precipitation and high temperature in chapter 2, and positions closer to the dry edge of the niche in chapters 3 and 4).

Drought-related conditions experienced before or after fire play a paramount role in the resilience capacity of Mediterranean tree species, and drought effects depend on the scale of the study and the used resilience measures. At the population level, my results show that pre-fire conditions warmer than those corresponding to the niche optimum (Chapter 2) or closer to the dry edge of the niche (Chapter 4) promote higher regeneration densities and thus maintain a drought-tolerant species, such as *P. halepensis* as the dominant species, the latter regardless of fire severity. However, warm and dry conditions after fire are negatively related to *P. halepensis* recruits' density (Chapter 2) although the species in most cases still preserves its pre-fire dominance in the ecosystem (Chapter 4). Yet, when the species is able to regenerate, such harsh conditions after fire may enhance the height of surviving recruits (Chapter 3) likely due to the mortality of individuals during extreme years, which may reduce inter- and intra-specific competition for resources. A similar pattern is found in thinning experiments in which low densities enhance the growth of pine trees (Turrión *et al*., 2022). Nevertheless, extreme drought conditions before and after fire (i.e., year of minimum distance to the dry edge of the climatic niche) can eventually promote shifts in the dominant species after fire even for a fire-adapted species such as *P. halepensis* (Chapter 4). In the case of *Q. ilex*, drought-related conditions promote the loss of dominance after fire, in agreement with studies that reveal the sensitivity of this species to dry conditions (Zavala *et al*., 2000). For *P. nigra*, drought-related conditions before the fire are marginally and negatively related to the loss of dominance, as expected in a drought-sensitive species (Martín-Benito *et al*., 2008). These cases illustrate that under the climate change context and considering the future scenarios where both fire and drought events are expected to be more frequent and intense (IPCC, 2023), understanding the effect of their compound regime on the resilience capacity of major tree species becomes essential.

The analysis of the impact of the warmest period (Chapter 2) or the driest conditions (Chapters 3 and 4) before and after fire provides relevant insights about the performance of a pioneer, typical Mediterranean species such as *P. halepensis*, in comparison to average annual variables or to distances to suboptimal conditions without discriminating the involved climatic variables (i.e., distance to niche edge instead of distance to the dry edge of the niche). The results illustrate the sensitivity of seedlings to extreme conditions, likely due to their incapacity to mobilize reserves (Baudena *et al*., 2020; Pausas & Keeley, 2014; Pratt *et al*., 2014) when these conditions occur after fire. They also point to the capacity of adult trees to relocate resources to resistance structures supporting key regeneration mechanisms, such as serotinous pinecones (Alfaro-Sánchez *et al*., 2015), when the drought occurs before fire (Chapters 2 and 4). In Mediterranean ecosystems, harsh conditions concur in the summer, the warmest and driest period, when high mortality rates of recently established plants commonly occur (Chapter 2) and the performance of recruiting individuals is reduced (Chapter 3). However, *P. halepensis* seems to compete better than the other studied species under summer-related conditions even in the early stages, being able to maintain dominance in the ecosystem after fire in many cases (Chapter 4).

As the case of *P. halepensis* demonstrates, the species' realized climatic niche framework used to explain the different measures of resilience gives us an idea of which is the resilience capacity of this species under the different climatic conditions that occur across its distribution range. In this PhD Thesis recruit performance indicative of resilience was characterized by several processes that involve different development stages (Grubb & Hopkins, 1986) of the tree, including primary growth, canopy growth or stress resistance (i.e., survival in the face of disturbances). The climate conditions in niche space that have a stronger influence in each of these stages can be assessed. Warm and dry conditions before fire increase regeneration density (Chapter 2) and promote the maintenance of *P. halepensis* as the dominant species (Chapter 4), probably due to the allocation of resources to seed production triggered by suboptimal drought-related conditions before fire (Alfaro-Sánchez *et al*., 2015; Espelta *et al*., 2011; Ne'eman *et al*., 2004). However, high variability in dry conditions after fire tends to reduce the cover of the *P. halepensis* regeneration, probably because fewer resources can be invested in primary growth (Chapter 4). On the opposite side, wetter conditions before fire seem to promote the recovery of the canopy cover after burning probably due to higher amount of resources that can be allocated within the surviving plants, allowing the storage of reserves favouring post-fire growth (Chapter 4). After the fire, the populations located in the driest area of the niche present lower density and height due to the suboptimal conditions that jeopardize the establishment and primary growth of seedlings (Chapters 2 and 3; Galiano *et al*., 2013; Pausas & Keeley, 2014). However, the dominance of *P. halepensis* in the ecosystem is largely due to the reduced competence with other tree species in these locations (Chapter 4, Zavala *et al*., 2000). My results also emphasize that the presence of extreme conditions (minimum distances to the dry or wet edge of the niche, Chapters 3 and 4) are also relevant, specifically after fire, to ecosystem resilience. Those may be related to the limit of the competence capacity of *P. halepensis* (Baudena *et al*., 2020). In addition to the climatic conditions, microsite characteristics also affect individual performance (Chapter 3). For instance, surface stoniness seems to limit *P. halepensis* primary growth, while intense intraspecific competition results in taller recruits with smaller basal areas and crown diameters.

The use of the deviation from the climatic niche optimum (Chapter 2) seems a suitable approach to explain the density of regeneration of *P. halepensis*, yet the distance to the edge of the realized species' climatic niche (Chapters 3 and 4) offers a strong predictor to understand the species response to compound fire and drought regimes. This could reflect that the optimum of this species' climatic niche, obtained from the distribution range of the adults, does not capture perfectly the optimum conditions for recruits, or that extreme conditions (closer to the climatic niche edge) constitute a stronger constraint to the regeneration dynamics of the species. Both the concept of the existence of a recruitment niche with a different shape, size and optimum position than the adult one and the importance of climate variability are in accordance with the studies that emphasize the climatic sensitivity of seedlings (Larson *et al*., 2023). However, for other species such as *Q. ilex* (resprouter) and *P. nigra* (fire sensitive) the distances to the optimum of the adult realized species' climatic niche are statistically significant to explain regeneration patterns, suggesting that the climatic niche built from adult occurrences would be appropriate to describe the climatic requirements for successful regeneration of these species. Another explanation of the better performance observed further from the niche optimum may be that the realized niche of the species, specifically the *P halepensis* ones, does not coincide with the fundamental niche, theoretically larger than the realized ones (Soberón & Nakamura, 2009), so when the conditions are closer to the physiological optimum, the species performance is good enough even if populations are in a suboptimal region of the realized niche.

Throughout this PhD Thesis, I have also evaluated the role of competition on population and individual-level resilience of three Mediterranean tree species with contrasted regenerative strategies. In the case of the seeder *P. halepensis*, at the individual scale (Chapter 3), the plant size of post-fire recruits does not seem affected by the presence of other species growing in the understory, such as *Quercus coccifera* or *Brachypodium retusum*. This may reflect that pine juveniles studied here were already taller than the surrounding vegetation layer of grasses and shrubs, minimizing competence for the light. However, the performance of *P. halepensis* recruits is significantly modulated by intra-specific competition, which leads to higher individuals with narrow stems and crowns, due to competition for light (Chapter 3). At the regional scale, the short-term maintenance of post-fire dominance suggests that *P. halepensis* is a good competitor after fire except when climatic conditions determine extremely dry years (i.e., corresponding to minimum distance to the dry edge of the species' climatic niche). Probably, in those extreme years, young recruits are particularly sensitive to drought, for instance, due to the still poorly developed root system and the lack of reserves (Chapter 4). Similarly, *Q. ilex* (resprouter) exhibits high resilience in suboptimal wet conditions except when extremely wet years occur after the fire (i.e., corresponding to minimum distance to the wet edge of the species' climatic niche). Under those conditions other species with faster growth rates may occupy the space more efficiently reducing, in turn, the competitive advantage of *Q. ilex* (Chapter 4, Bussotti & Pollastrini, 2020).

To summarize, we found a relationship between niche metrics and resilience measures, considering demographic variables (density of regeneration, performance of the recruits, vegetation recovery and species dominance in the ecosystem). The findings thus indicate that the climatic niche offers a conceptual framework that could contribute to towards better understanding and prediction of populations' performance after disturbance, considering different spatiotemporal scales (i.e., from individual level to regional landscape). However, individual responses at smaller spatial scales where the role of microsite characteristics, such as surface stoniness and intraspecies competition (Chapter 3, Del Campo *et al*., 2007; Mendez-Cartin *et al*., 2024), gain importance should not be uniquely explained by niche position.

5.2 Fire severity-climate interactions and resilience

Severity is a fire characteristic modulated by several variables such as fuel load, structure and moisture, wind speed and vegetation flammability (Flannigan *et al*., 2013). In this PhD Thesis, I found that the wildfire severity affects differently the resilience of the studied species. In the case of *Q. ilex* and *P. nigra* (Chapter 4), high-severity wildfires result in the short-term loss of their dominance across the Iberian Peninsula. For *P. halepensis* populations growing on the eastern coast of the Iberian Peninsula, wildfire severity explains high regeneration rates, measured as recruit density (Chapter 2). However, when considering the entire Iberian Peninsula distribution of *P. halepensis* (Chapter 4), fire severity does not show a significant relationship with the measured resilience variables. This contrasting pattern at different spatial scales may be related to the relationship between severity and the climatic quality of sites (i.e., areas burned by low-severity wildfires are likely to occur in wetter sites, Supplementary Material Figure SM5.1) where more intense competition is more likely to occur, jeopardizing successful recruitment. So, although severity alone cannot explain species regeneration, it should be considered when interpreting local patterns of post-fire regeneration (Karavani *et al*., 2018).

In agreement with classic fire ecology, my results confirm that the existence of regeneration strategies adapted to the fire regime is a key determinant of the resilience of the populations (Chapter 4, Coop *et al*., 2020). In the case of *P. nigra*, seeds are sensitive to heat, preventing successful post-fire regeneration (Retana *et al*., 2002), thus favouring its replacement by other species such as *Quercus pubescens* (Chapter 4). *P. nigra* losses dominance in most of its locations after the fire (it only remained dominant in 22.5% of the burned plots assessed), and population decline increases with time after the fire, indicating that even the surviving populations can be eventually replaced by other species better adapted to post-fire conditions, or with more efficient post-fire regeneration mechanisms (Chapter 4). In contrast, both *P. halepensis* and *Q. ilex* can be considered fire-prone species, although they show substantial differences in their post-fire regeneration strategy. Contrary to our expectations, the resprouter *Q. ilex* appeared highly affected by fire severity, probably due to the damage to the underground buds, particularly in dry conditions (Parra & Moreno, 2018). In addition, resprouts would require some degree of humid conditions after the fire to successfully recover canopy cover, in contrast with expectations of certain independence of growth from climate conditions thanks to the mobilization of root reserves in lignotubers and roots (Clarke *et al*., 2013). On the other hand, the seeder *P. halepensis* exhibited high resilience to wildfire, even under high-severity fire events (Chapter 2). In addition, the response of this seeder species to post-fire dry conditions depends on the spatiotemporal scale and the type of variable considered. Drought-related conditions after fire seem to jeopardize the density and height of the recruits, making them less competitive (Chapters 2 and 3), due to the sensitivity of seedlings to harsh climatic conditions. However, the lack of competence with other tree species under dry conditions may allow the maintenance of *P. halepensis* dominance in the ecosystem (Chapter 4).

5.3 Limitations and future research

The studies that compose this PhD Thesis have demonstrated that the use of realized species' climatic niche is a useful tool to explain the resilience of Mediterranean tree species after wildfires. However, the selection of the dataset of the species distribution used to build the environmental climatic space can determine the explanatory capacity of the models. In our approach, the lack of data from the North African distribution range can underestimate the niche of the species under study, especially for drier-hotter conditions. Although the use of the Spanish forest inventory and the EUforest dataset can provide enough occurrence for temperate species, the analysis of Mediterranean species may benefit from considering species occurrence in the entire Mediterranean Basin. In addition, the difference in plot selection and survey protocols, including survey frequency and plot size, can be a source of variability, hampering the use of occurrence compilations such as EUForest or GBIF. As my results demonstrate, the limits of the realized species' climatic niche (i.e., wet and dry edges of the niche) constitute an important element to understanding the resilience capacity of species. Therefore, the construction of the species' realized niche including comprehensive occurrence records in their broader, significant range appears as a future step to strengthen this technique.

The distribution of tree species in Europe is strongly affected by the anthropization of the landscapes. In some areas during the last centuries, the presence of forest species has been promoted or dismissed following human imperatives such as wood production, land use for agricultural needs or human settlements and reforestation programs (Bogaert *et al*., 2014). Human-induced modification of species distribution areas could make estimations of species' realized niches substantially different from the ones that they would exhibit in natural conditions. So, we would have to consider this bias when constructing the realized climatic niche of the species. Some steps to ameliorate this issue could be the removal or weighting of plantations from the species occurrence set. For this task, it would be essential to correctly identify past management in the inventories, but this is often difficult to recognize in the field, depending on the time since the reforestation. Since this type of information is provided to some extent in the IFN, the niche constructed with these occurrences (Chapter 2) did not include reforested plots. But in the case of the niches constructed with the EUForest dataset (Chapters 3 and 4), this information is not provided (Mauri *et al.*, 2016b), hence all the occurrences were included in these cases.

Despite the large number of plots included in the IFN for the three species under study, the filters applied in Chapter 4 to select burned plots (i.e., 50% of their surface covered by the target species and areas burned only once in the last twenty years before the last inventory) derived in a small number of replicates for *P. nigra* and *Q. ilex*. This situation results in a heavy dependence on stochasticity that may have prevented obtaining more explicative models. Despite this shortcoming, some explanatory variables exhibited statistical significance in the models, supporting the soundness of the approach. The inclusion of neighbouring Mediterranean areas, such as Portugal or France could be a solution to increase the number of study plots, although the disparity between the survey procedures should be standardized. Additionally, the inclusion of subsequent IFN campaigns (i.e., IFN4) would allow corroboration of the short-term resilience trends assessed in Chapter 4.

In the last decades, a change in the climatic conditions worldwide is happening, due to the increment in the temperatures, the reduction and concentration in the time of the rainfalls, and an increment in the frequency of extreme climatic phenomena (IPCC, 2023). In this context, the survival and growth patterns of the species, especially regenerating populations, could be compromised (Solomou *et al.*, 2017). For the studied species, the increment of the dry conditions could imply the reduction or disappearance of populations of *Q. ilex* or *P. nigra* associated with the loss of dominance in forest communities (Chapter 4). In the case of *P. halepensis,* the effects will depend on when the dry conditions occur. Overall, we can expect maintenance of *P. halepensis* dominance (Chapter 4) but probably with lower densities or with individuals with lower growth rates and smaller sizes (Chapters 2 and 3). The composition and structure of the vegetation have also changed in the last decades due to the modifications of land use. In the European context, the abandonment of rural areas, the intensification of agricultural practices (e.g., intensive livestock farming, irrigation) and the successful fire suppression policy have promoted the increment of the forest biomass, leading to vertical and horizontal continuity of fuel, thus favouring wildfires (Pausas & Keeley, 2021). The accumulation of fuel together with the increment of the temperatures, particularly in summer, makes high-intensity fires with a larger burned area more likely across the European territory (El Garroussi *et al.*, 2024; Seidl *et al.*, 2017). Under this scenario, the resilience of *P. halepensis* is, overall expected to remain in the Iberian Peninsula, but at a local scale, the increment of fire severity could result in denser populations (Chapter 2). For the other studied species, the increment in fire severity could, thus, imply the loss in their dominance, which may be indicative of a future decline of their populations, particularly for *P. nigra*.

5.4 Concluding remarks

This PhD Thesis provides evidence that the approach based on realized species' climatic niche is useful for assessing Mediterranean forest resilience, measured as the density of regeneration, recruits growth, and maintenance of the dominance or recovery of the canopy cover, across species and regions. Distance or deviation from the optimum of the realized species' climatic niche is a useful variable to explain the resilience of Mediterranean tree populations. Importantly, the distance to the niche edge gains explanatory capacity when it is referred to particular, relevant bioclimatic variables, such as those related to drier or wetter conditions. Also, the use of the warmest quarter variables (i.e., corresponding to summer) to build the niche provides greater explanatory capacity to the models. Moreover, microsite characteristics, such as surface stoniness or intraspecific competition, have also a relevant influence on population resilience when the study resolution scales down, particularly at the individual level.

The capacity of the studied Mediterranean forests to recover after wildfires is largely determined by the regeneration strategy of their dominant species. In the case of *P. halepensis* and *Q. ilex* it corresponds to high recruitment and resprouting, respectively. In the case of *P. nigra*, a species without efficient post-fire regeneration mechanisms, the few plots that maintain the dominance of this species are likely due to the enhanced growth after the wildfire of the surviving trees. However, drought-related conditions before and after the fire significantly modulate the resilience of the populations to wildfires. Therefore, the regeneration capacity of species must be evaluated in the framework of compound fire-drought regimes.

Since the resilience capacity of species is influenced by the climatic conditions as translated into their realized climatic niches, resilience could diminish under climatic change scenarios implying an approximation towards the climatic conditions corresponding to the dry edge of the niche. However, other factors such as species' competitive capacity should be considered when assessing changes in ecosystem-level dominance.

Supplementary material

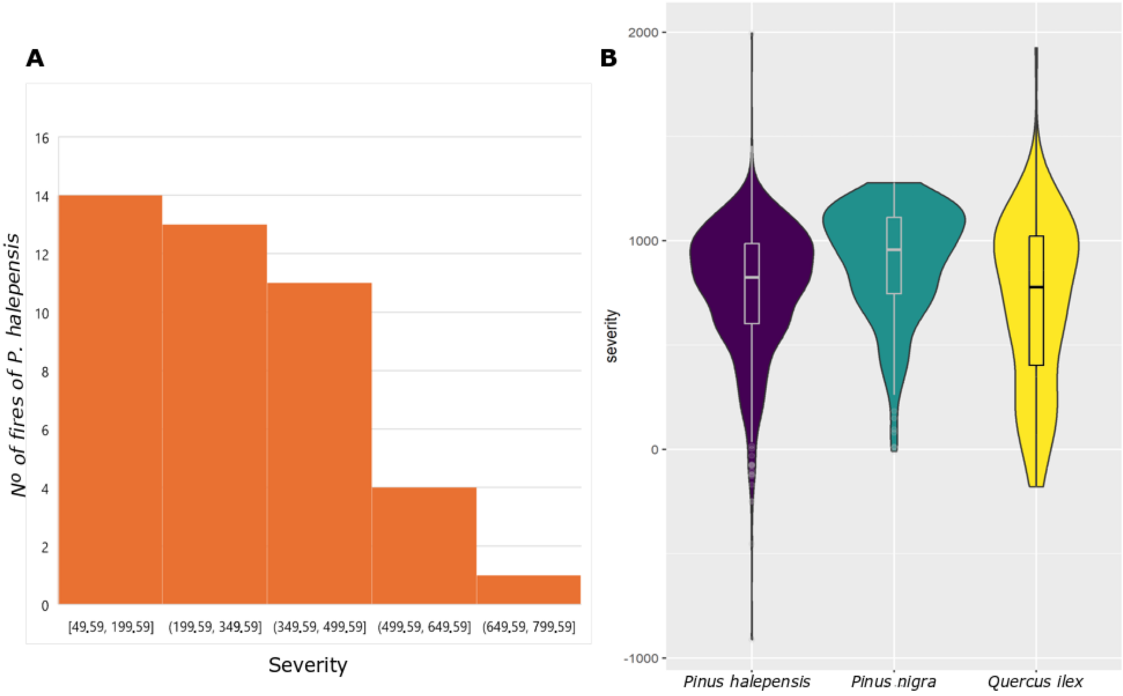


Figure SM5.1: Severity of the fires for the plots of *Pinus halepensis* in Chapter 2 (A) and for the plots of the three species in Chapter 4 (B).

General conclusions

Chapter 2

- Post-fire regeneration density in *Pinus halepensis* is determined by the deviations from the optimum of the realized species' climatic niche previous and posterior to the wildfire in interaction with fire severity.
- Warmer conditions before fire enhances pine recruitment likely due to higher production of seeds and increased serotiny, but the opposite occurs if warmer conditions occur after wildfire because drought-related conditions are expected to have higher influence on recruits' survival.
- Wetter conditions after wildfire also promote pine recruitment because seedlings are more sensitive to changes in resources availability, particularly to water in Mediterranean-type ecosystems.
- High-severity fires are related to higher densities of regeneration in *P. halepensis* but the interaction with the climatic conditions can modify this relationship.
- The influence of climate conditions related to drought episodes is better assessed when they are referred to the species' climatic niche than to raw climatic measures.
- The models analyzing the role of species niche on regeneration are more explicative when they consider more extreme climatic conditions, such as the warmest period, than when they consider the annual variables.

Chapter 3

- Population location within the realized species' climatic niche and especifically in relation to the dry edge of the niche (reflecting wamer and drier conditions) appear as suitable metrics to explain the performance of post-fire regeneration in *Pinus halepensis*.
- Primary growth (i.e., height) is the resilience metric more related to the position within the niche, compared with basal area, diameter of tree crown and percentage of green canopy.
- Recruits height is significantly and positively related to the distance to the dry edge of the niche, so drier conditions after fire result in smaller recruits.
- The presence of extremely dry conditions results in taller recruits probably due to the filtering effects that allow access to more resources for surviving plants.
- Competition with other small-sized species do not affect the performance of the individuals in the sapling stage, but it probably affects early stage such as germination or seedling establishment.
- Microsite characteristics such as soil stoniness or intraspecific competition also exert a significant influence on recruits performance.
- The performance of recruits is better explained when considering distances to the dry edge of the niche than when considering distances to the niche edge merely.

Chapter 4

- The presence of a fire-prone regeneration strategy determines the resilience of tree populations in front of wildfires, characterized as the maintainance of the species' dominance in the community.
- The position of the populations in the realized species' climatic niche, especially the distance to the wet and the dry edges of the niche, modulate the post-fire resilience of *Pinus halepensis*, *Quercus ilex* and Pinus *nigra*.
- For *P. halepensis* the occurrence of drought-related conditions before and after fire enhances the maintaniance of its dominance but the presence of extremely dry years lead to the loss of it.
- *Q. ilex* maintain ecosystem dominance when wet conditions occur after fire, but the occurrence of extremely wet years enhances species shift.
- The resilience of *P. nigra* is mainly affected by the severity of the fire, as high-severity fires cause the loss of its dominance regardless of pre- and post-fire climate conditions.
- In the context of climatic change, where more frequent and intense droughts are expected, *P halepensis* seems to be the most resilient species.

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