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

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ABSTRACT

Understanding how climate and fire severity affect post-fire regeneration in Mediterranean vegetation is essential to assess population resilience under increasing fire and drought events linked to climate change. We examined three tree species—*Pinus halepensis*, *Quercus ilex*, and *Pinus nigra*—with contrasting post-fire regeneration strategies, to explore how climatic conditions within their realized niche influence canopy recovery in burned areas. Species' climatic niches were defined using EU Forest Inventory data and 12 bioclimatic variables (1979–2018), projected onto a principal components (PCA) space. We identified each species' niche core using kernel density estimation, and delineated wet and dry edges based on bioclimatic contributions to the first two PCA axes. Using plots from the Spanish National Forest Inventory (IFN), we selected areas dominated by the target species in IFN2 (1986–1996) that burned before IFN3 (1997–2007) and extracted pre- and post-fire canopy cover and species dominance. We modelled changes in canopy and dominance as a function of climatic distance from niche core and edges, incorporating fire severity. *Pinus halepensis* maintained post-fire dominance under drier conditions, while wet post-fire conditions enhanced canopy recovery. *Quercus ilex* increased in dominance under wetter post-fire climates. *Pinus nigra* was largely replaced post-fire, though wet-edge conditions occasionally supported its persistence. Fire severity affected dominance shifts in *P. nigra* and *Q. ilex*, but not in *P. halepensis*, reflecting its adaptation to high-severity fires. Our findings highlight how niche position and fire severity jointly shape post-fire regeneration, with implications for predicting species' resilience under climate change.

1. Introduction

Forest fires 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 fires 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 fires.

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 fire regimes (Beckage et al., 2009; McLauchlan et al., 2020). In the Mediterranean Basin, there are two dominant, not mutually exclusive, fire-recovery strategies (Pausas and Keeley, 2014). On the one side, seeder species, with abundant seedling recruitment after fire, focus their reproductive effort on seed production.

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On the other side, resprouter species exhibit vegetative growth from surviving parental tissues such as roots, rhizomes or lignotubers. Plant species can show one of these responses, exhibit both of them (facultative species) or be fire-sensitive with populations dependent on colonization processes (Keeley et al., 2011). However, large extents of severely burned land can limit tree regeneration after fire, even for fire-adapted species. This may be due to the destruction of protected buds and reserves in sprouting species, and to the depletion of seed banks and long distances from seed sources (unburned forest) in seeding species (Coop et al., 2020; Davis et al., 2019; Karavani et al., 2018; Ordóñez et al., 2005). This regeneration failure eventually results in changes in tree canopy cover.

In addition to fire regime characteristics, post-fire climatic conditions can determine the success of tree regeneration, from the establishment and the regrowth of trees, thus, determining the recovery of canopy cover (Batllori et al., 2019; Baudena et al., 2020). Climatic conditions can be characterized through the species' climatic niche, which offers an appropriate framework to assess species' response to disturbance (Díaz-Borrego et al., 2024; Jaime et al., 2019; Margalef-Marrase et al., 2022). Therefore, regeneration success after fires can be explained by the location of the population in the climatic niche of the species (Elvira et al., 2021). For instance, populations historically located near the edge of the climatic niche tend to show lower performance, and the reversal pattern is expected in conditions closer to the niche core (Elvira et al., 2025).

This study aims to assess whether pre- and post-fire populations' position in the climatic niche space affects the recovery of post-fire canopy cover and changes in species dominance in forests formerly dominated by a single species. We studied three species typical from the western Mediterranean Basin, *Pinus halepensis*, *Quercus ilex* and *Pinus nigra*, with distinct regeneration strategy: seeding, resprouting and fire-sensitive, respectively. In this region, recent changes in fire behaviour, with a greater frequency of large, high-intensity fires (Aldersley et al., 2011; Alvarez et al., 2024), are occurring under increasing drought conditions (Chergui et al., 2017; Ordóñez et al., 2005) and this may jeopardize post-fire regeneration. We analysed changes in canopy cover and species dominance in plots surveyed in the Spanish National Forest Inventory (IFN) before (IFN2) and after fires (IFN3) in relation to fire severity and pre- and post-fire climatic conditions typified through the species' climatic niche. The Euclidean distance of burned populations to the respective climatic niche optimum (i.e., niche core or centroid) and to the wet and dry edges were used to characterize pre- and post-fire climatic conditions. Our main hypothesis is that population position in niche space (i.e., distance to niche core and edges) will modulate their response to fire, with those populations growing in locations close to the niche core and far from the dry edge of the species niche exhibiting higher canopy cover. Also, we expect that the post-fire regeneration strategy will explain the relationship between populations' position in the niche space and the recovery of canopy cover following fire.

2. Material and methods

2.1. Species of study

We studied three of the most common tree species of Mediterranean forests in the Iberian Peninsula, which are representative of distinct regenerative strategies following fires. *Pinus halepensis* Mill. is an obligate seeder with a canopy seedbank that persists through effective recruitment of seedlings, *Quercus ilex* L. resprouts after fire and *Pinus nigra* J.F. Arnold is considered fire-sensitive. Aleppo pine (*P. halepensis*) is the most thermophilic and abundant pine under Mediterranean climates in the western Mediterranean Basin (Rouget et al., 2001). It produces serotinous and semi-serotinous cones that accumulate a crown seed bank that is released by fires, 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 promote crown defoliation and branches dieback (Pollastrini et al., 2019). The underground parts of holm oak survive fires and provide the resources to the dormant buds to resprout vigorously afterwards (Clarke et al., 2013; Retana et al., 1992). Black pine (*P. nigra*) shows the most Eurosiberian distribution of the three studied species. After fire, this species not have an effective strategy to persist, thus being obligated to colonize burned sites from surviving trees in unburned patches or nearby forests (Espelta et al., 2002).

2.2. Plot sites selection

We obtained fire perimeters in the Spanish Iberian Peninsula's territory between 1986 and 2018 from the fire database compiled by Alvarez et al. (2024). We selected those plots in the Spanish National Forest Inventory (IFN), included within the fire perimeters, in which the studied species were dominant (canopy cover $\geq$ 50 %) and that were burned only once between the successive samplings of IFN2 (1986–1996, Villaescusa and Díaz, 1998) and IFN3 (1997–2007, Bombín and Cezón, 2018) (Fig. 1). We obtained 644 plots for *P. halepensis,* 107 for *Q. ilex* and 225 for *P. nigra.* To estimate the fire severity in each plot, we first calculated severity within the burned area of each study site using Google Earth Engine®, following the methodology described in Parks et al., (2018) (https://code.earthengine.google.com/c76157be827be2f24570df50cca427e9; last accessed 10/05/24). The differenced Normalized Burn Ratio (dNBR) was generated using Landsat TM, ETM+ , and OLI imagery, which includes the near-infrared (NIR) and shortwave infrared (SWIR) bands.

2.3. Canopy cover metrics

We assessed if there has been a change in canopy cover within the study plots after fire comparing the two IFN2 and IFN3 surveys using two metrics. We defined species dominance shift as a binary variable where 0 represents the maintenance of the dominance of the focal species (at least 50 % of the plot canopy cover in both surveys) and 1 represents that the dominant focal species in IFN2 had less than 50 % of the plot canopy cover in IFN3. We also considered the change in canopy cover: the difference in the percentage of the canopy cover of the pre-fire dominant focal species between IFN3 and IFN2. This metrics (IFN3 cover minus IFN2 cover) is a proxy of resilience *sensu* (Lloret et al., 2011). So, values close to zero indicate high resilience, while more negative values indicate lower resilience. Positive values indicate an increment of the canopy cover relative to pre-fire conditions, suggesting that the fire enhanced the canopy cover of the focal species; this situation is not expected given the short term between the fires and the IFN3 survey.

2.4. Climatic niche characterization

We characterized species' climatic niches according to their European distribution range using the high-resolution pan-European tree occurrence inventory (EUForest - Mauri et al., 2016) and monthly climatic data obtained from CHELSA (ver 2.1 Karger et al., 2017, period 1979–2018). We extracted the monthly climate data from all geographic locations of each species (13,121 occurrences for *P. halepensis*, 883,779 occurrences for *Q. ilex* and 415,428 occurrences for *P. nigra*) and then computed the yearly climate values of twelve bioclimatic variables characterizing temperature and precipitation regimes (Supplementary material Table SM1). The use of yearly values for each location instead of a single averaged value for the 1979–2018 period allows for a better characterisation of the inter-annual variability in environmental conditions experienced by species, and captures the extreme year values that could be underrepresented using only one value for the entire period (Pérez-Navarro et al., 2020).

We characterized the climatic space occupied by each species using



Fig. 1. Location of the IFN plots burned between IFN2 and IFN3 surveys across the Spanish Iberian Peninsula's territory, which were dominated by the species under study.

the combination of the twelve bioclimatic variables, reducing their dimensionality into multivariate axes using Principal Components Analysis, PCA (Broennimann et al., 2012). The contribution of the 12 bioclimatic variables within the axes that characterized the niche of each species is available in Fig. 2 and Supplementary Material Table SM2.

The density distribution of each species' occurrences within the respective climatic space was computed through kernel density estimates (i.e., the realized climatic niche, Broennimann et al., 2012). The species' climatic core was computed as the centre of mass of occurrence density in climatic space, which corresponds to the point of highest species density within the climatic niche. Also, the limit of the species' climatic distribution (also named niche edge) was calculated using the 95 % density kernel. We used 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 (Fig. 2) characterized by higher temperatures, higher temperature, seasonality and lower precipitation (positive contribution of bioclimatic variables Bio 1, 4, 5, 6, 10, 11 and 15; negative contribution of bioclimatic variables Bio 12, 13, 14 and 16) and a wet edge of the niche characterized by lower temperatures and higher precipitation (positive contribution of bioclimatic variables Bio 12, 13, 14, 16 and 17; negative contribution of bioclimatic variables Bio 1, 4, 5, 6, 10, 11 and 15). Following the methods described in Elvira et al. (2025), we used the projections (red shaded in Fig. 2 A, C and E) of the bioclimatic variable Bio 4 and Bio 6 on the niche edge contour to define the dry edge (red contour in Fig. 2 B, D and F), and the projections of the bioclimate variable Bio 14 and Bio 16 (blue shaded in Fig. 2 A, C and E) to define the wet edge (blue contour in Fig. 2 B, D and F).

Finally, we projected within the species' climatic niche the coordinates of the selected IFN plots for the 5 years before the fire and for all the years between fire occurrence and the IFN3 survey. For each of these points (i.e., IFN plot and year) we calculated the Euclidean distance to the niche core and to the closest point of the wet and the dry edges of the niche (Fig. 2). We computed the mean and the standard deviation of the distances to niche core for the pre- and post-fire periods. To standardize niche metrics among species with different niche areas, we weighted the distances (WD) to the niche core by the respective distance to the niche edge as $WD=DC*(DC+DE)^{-1}$ where *DC* and *DE* correspond to the distance to the core 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 the niche space. So, points within the niche will have a weighted distance ≤ 1 and points outside the niche a weighted distance > 1. We also calculated the minimum, the mean, and the standard deviation of the distances to both edges of the niche (wet and dry) for the pre- and post-fire periods. The minimum distance captures the extreme climatic conditions experienced by populations during the considered period, the mean distances reflect the general conditions, and the standard deviation inform about the variability in the climatic conditions relative to the dry and the wet edge of the niche. Distances to the wet and dry edges were not weighted by the distance to the core assuming that population performance will be sensitive to absolute distances to the limits of the climatic requirements, irrespective of the distance to optimal conditions.

R package ade4 (version 1.7–22, Dray and Dufour, 2007) was used to perform the PCA. R packages ks (version 1.10.7, Chacón and 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 core and edge.

2.5. Statistical analysis

Two models for each species were used to assess the relationship between canopy cover metrics after fires in relation to the position of burned plots in the species niche space. In the models, the response variables were species dominance shift and change of canopy cover. Predictor variables included the mean and standard deviation of the pre- and post-fire weighted distances to the niche core, as well as the mean, minimum and standard deviation of distances to the wet and dry edges of the niche. In all models, severity and time since fire (i.e., years between fire and IFN3 inventory) were also included as predictor variables. For *P. halepensis* models and *Q.ilex* canopy cover changes' model fire identity was included as a random effect in mixed models (GLMM) as it improved the hierarchical structure without adding unnecessary complexity. The rest of relationships were assessed through generalized linear models (GLM) to avoid overparameterization or convergence issues.

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

3. Results

Both *P. halepensis* and *Q. ilex* remained as the dominant species in most of the burned plots (74.5 % out of 644 burned plots, and 73.8 % out of 107 burned plots, respectively, Supplementary material Figure SM1 and Table SM3), while *P. nigra* only remained as the post-fire dominant species in 22.5 % of its 225 burned plots (Supplementary material Figure SM1 and Table SM3). Where it regenerates, *P. nigra* have in general less change of canopy covers relative to pre-fire forest than *P. halepensis* and *Q. ilex*, although these two species showed higher intraspecific variability for this variable (Supplementary material Figure SM2).

In *P. halepensis* models, species dominance shift has a positive, significant relationship with the mean distance to the dry edge of the niche before fire (p-value <0.05, Fig. 3, Supplementary material Table SM4), with the standard deviation of the weighted distance to niche core 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

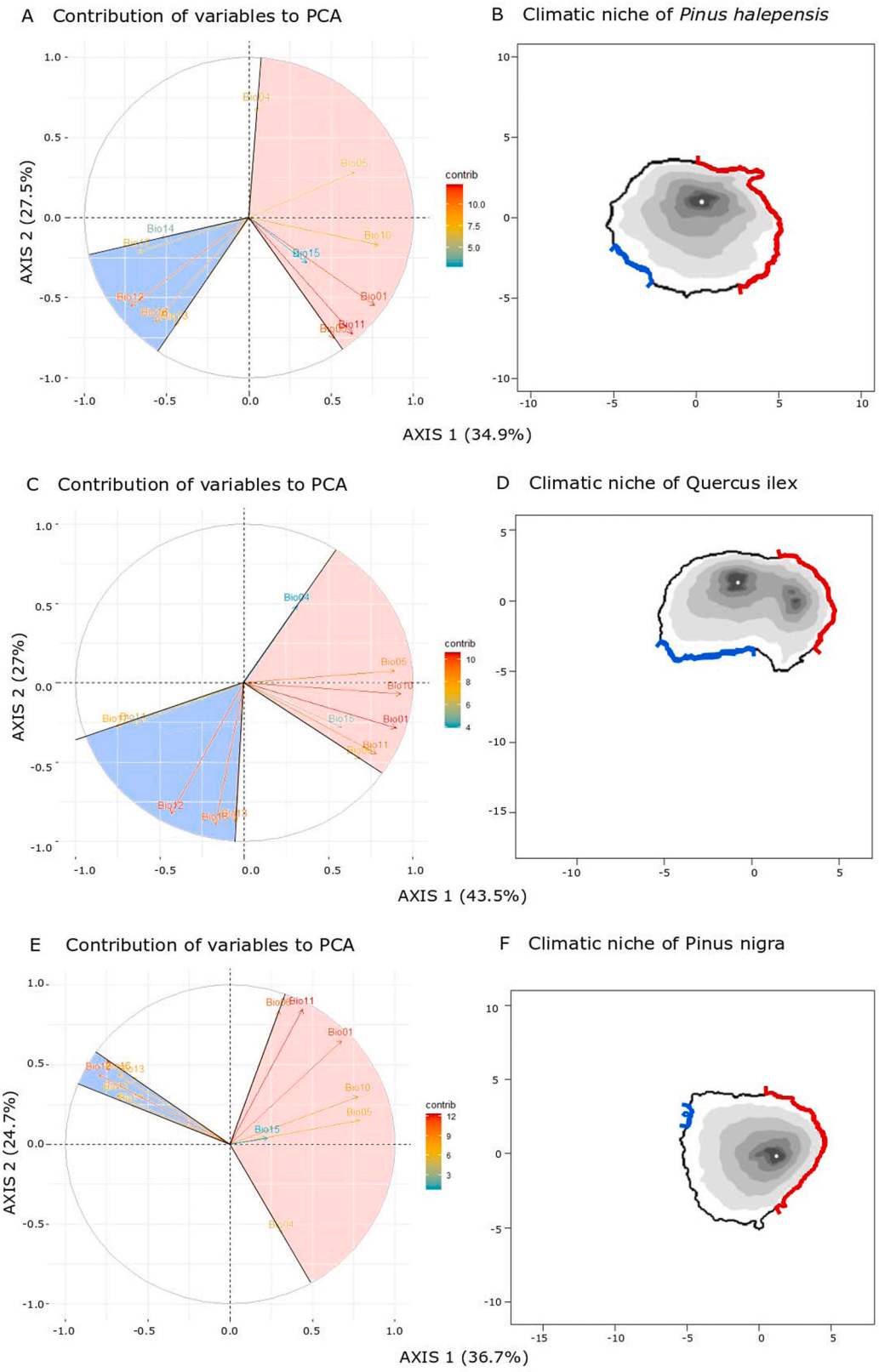
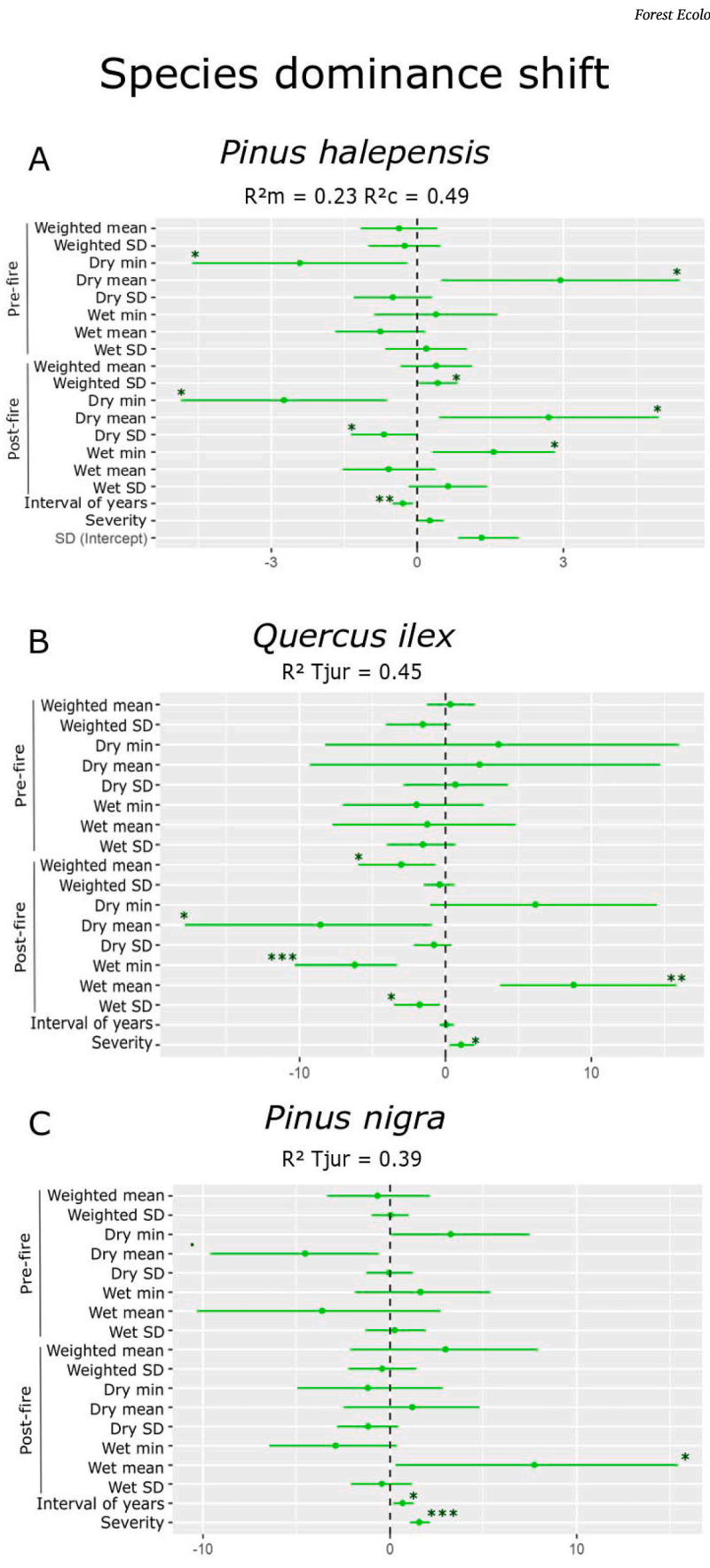


Fig. 2. Correlation circles obtained from the principal component analysis (PCA) performed with twelve selected bioclimatic variables describing the geographical locations in which *Pinus halepensis* (A), *Quercus ilex* (C) and *Pinus nigra* (E) have been recorded in the EUForest database (Mauri et al., 2016). Colour arrows indicate the contribution of each variable. Red shaded area indicates the arc that delineates the dry edge while blue shaded area indicates the equivalent for the wet edge. The realized climatic niche is shown in panel B, D and F, where the white dot represents the niche core, and the red and blue borders indicates the dry and wet edges of the niche, respectively.



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Fig. 3. Results of the models for species shift after fire for the studied species in relation to distances to the climatic niche core (Weighted mean, Weighted SD), the dry niche edge (Dry min, Dry mean, Dry SD), and the wet niche edge (Wet min, Wet mean, Wet SD), as well as fire severity and time since fire (interval of years). See Table SM 7 for a full description of the predictor variables. A) *Pinus halepensis*, B) *Quercus ilex,* C) *Pinus nigra*. R^2m corresponds to the Pseudo-R^2 (fixed effects) while R^2c corresponds to Pseudo-R^2 (total), R^2Tjur corresponds with the Tjur coefficient of discrimination. 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.

<0.05), with the standard deviation of the distance to the dry edge after fire (p-value <0.05), and with the number of years between the fire and the post-fire plot inventory IFN3 (p-value <0.01). The change of *P. halepensis* canopy cover after fire was negatively related to the standard deviation of the distance to the dry edge of the niche before fire (p-value <0.1, Fig. 4, Supplementary material Table SM4), to the mean distance to the wet edge of the niche before fire (p-value <0.01) and to the mean weighted distance to the niche core after fire (p-value <0.01). It was also positively related to the mean weighted distance to the niche core before fire (p-value <0.01), to the minimum distance to the wet edge before fire (p-value <0.01) and to the standard deviation of distance to the wet edge before fire (p-value <0.01).

In *Q. ilex* model, species dominance shift showed a negative, significant relationship with the mean weighted distances to the niche core after fire (p-value <0.05, Fig. 3, Supplementary material Table SM5), 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 standard deviation of the distances to the wet edge after fire (p-value <0.05). It also had 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 change of *Q. ilex* canopy cover after fire showed only a significant relationship with the mean weighted distance to the niche core after fire (p-value <0.01, Fig. 4, Supplementary material Table SM5).

In *P. nigra* models, species dominance shift exhibited a positive relationship with mean distance to the wet edge after the fire (p-value <0.05, Fig. 3, Supplementary material Table SM6), 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 and significant 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 canopy cover change in *P. nigra* plots (Fig. 4, Supplementary material Table SM6)

4. Discussion

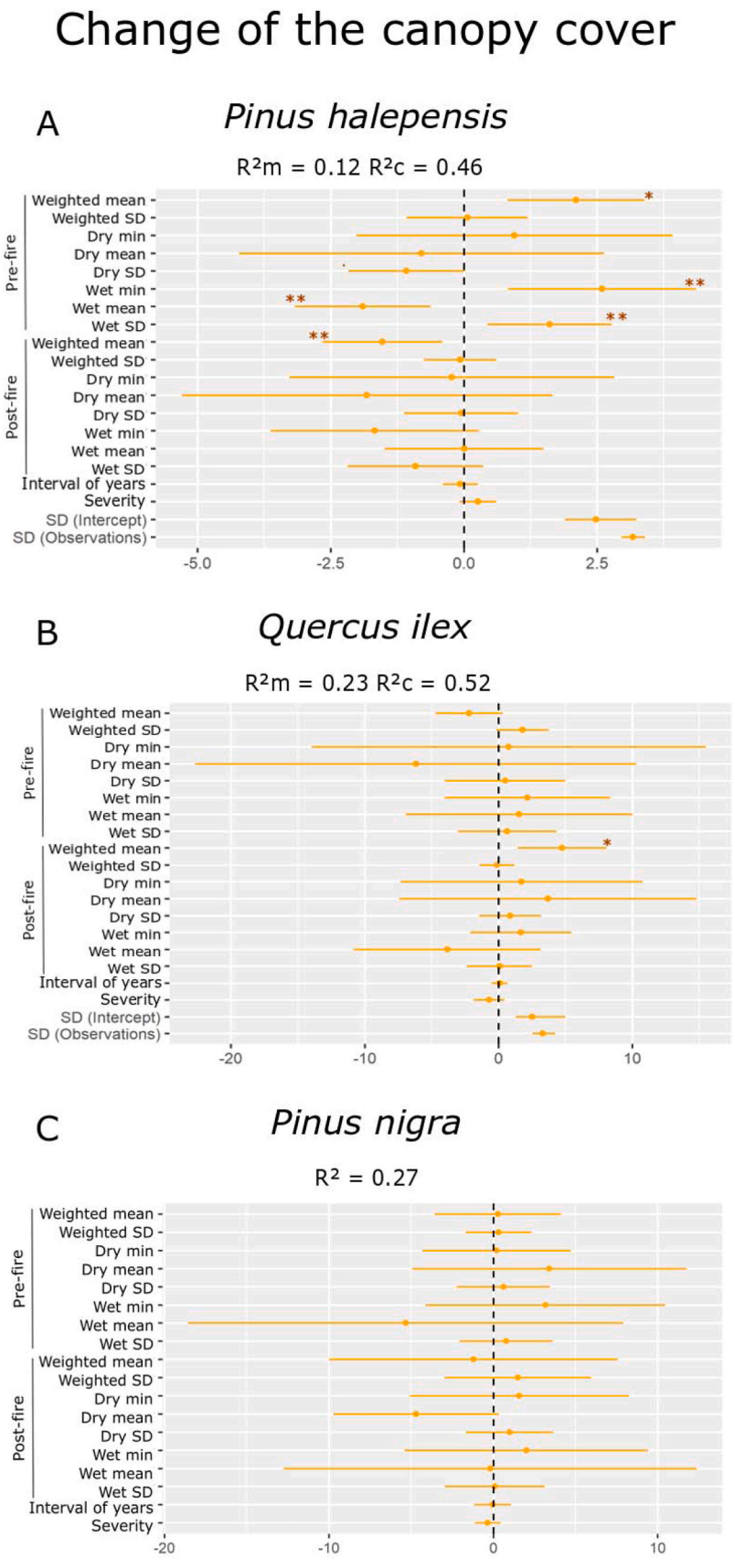
Here we report the importance of populations' location within the species' realized climatic niche (distance to niche core and edge) to understand the short-term shift in species dominance and change in species' canopy cover in Mediterranean burned forests. Although these changes are not necessarily 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, shape long-term dynamics. Our results also corroborate the importance of regenerative strategies for post-fire recovery (Enright et al., 2014). These results shows post-fire maintenance of tree species dominance in species exhibiting post-fire regenerative strategies, by resprouting from underground buds in *Q. ilex*, or by the establishment of new plants from seeds released by serotinous cones in *P. halepensis* (Clarke et al., 2013; Núñez and Calvo, 2000). The efficiency of these mechanisms resulted in the persistence of these fire-adapted species as dominant in around 75 % of the burned plots. In contrast, *P. nigra* burned plots suffered more frequently (ca. 80 %) a shift in the dominance of this species, thus reflecting its fire-sensitive character and low resilience to fires (Ordóñez et al., 2005).

Fire severity explains the shift of dominant species in the case of *P. nigra* and *Q. ilex*, but not in *P. halepensis*. This supports the notion that the latter is well adapted to stand replacing fires, even when they burn standing trees (Parra and Moreno, 2018). However, the success of *P. halepensis* post-fire establishment has been reported to be dependent on other variables, such as post-fire climatic conditions, 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 and Keeley, 2014). Although communities dominated by seeder species may show heavy impact on their structure under highly intense fires, compared with resprouters (Jimeno-Llorente et al., 2023), the establishment of new cohorts, such as in *P. halepensis*, may enhance their dominance in the mid-term regardless of the severity of the fires.

However, *P. halepensis* showed replacement by other species in sites where pre-fire climatic conditions were further from the dry edge of the climatic niche (i.e., higher mean distance to the dry edge of the niche). Therefore, our assessment reveals that more humid conditions before the fire promoted a post-fire shift to other species, such as *Q. ilex* or *Arbutus unedo,* that relates to later successional stages (Supplementary material Table SM3). In contrast, the locations closer to the dry edge of the niche of *P. halepensis* may be suboptimal for other potentially replacing species. In addition, in semi-arid locations, *P. halepensis* increases the production of serotinous cones (Alfaro-Sánchez et al., 2015), which favours the maintenance of its dominance after fire. 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 for post-fire recovery. In fact, in our case, extremely dry years were associated with shifts to other species such as *Juniperus oxycedrus*, which may find their optimal distribution in drier conditions than *P. halepensis* (Supplementary material Table SM3). The occurrence of dry, post-fire conditions on average (i.e., smaller mean distances to the dry edge of the niche) were also relevant in promoting *P. halepensis*' dominance. This species is one of the most xerophilic tree species in the Iberian Peninsula (Rouget et al., 2001), so favourable dry conditions for this species are likely to be unfavourable for other species, thus giving competitive advantage to *P. halepensis* recruits (Zavala et al., 2000). On the other hand, although seedling mortality related to drought would leave more resources for *P. halepensis* survivors (Elvira et al., 2025; Turrión et al., 2022), under extremely dry conditions after fire the recruits density would not be high enough to maintain the species' dominance (Elvira et al., 2021).

The recovery of the canopy cover of burned *P. halepensis* forests was favoured in populations where conditions were distant from the niche core but closer to the wet edge of the niche during pre-fire years. This may be due to denser canopy cover in surviving trees which could have stored abundant reserves during wet years before fire (Santini et al., 2019). However, years with minimum distances to the wet edge of the *P. halepensis*' niche impose difficulties for the recovery of the canopy cover after fire, probably because, under such wet conditions, other species may be more competitive (e.g., *Quercus* spp.). This pattern agrees with its higher recruits' performance after fire in sites with larger mean distances to the dry edge of the species niche (Elvira et al., 2025). Recruits may be very sensitive to favourable conditions that could thus promote faster growth and species cover (Royo et al., 2001).

These models provide, overall, insights into the post-fire recovery capacity of *P. halepensis* 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 result in a greater production of structures (serotinous cones) that allow the species to remain after the fire (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



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Fig. 4. Results of the explanatory models for the change of the canopy cover for the studied species in relation to distances to the climatic niche core (Weighted mean, Weighted SD), the dry niche edge (Dry min, Dry mean, Dry SD), and the wet niche edge (Wet min, Wet mean, Wet SD), as well as fire severity, and time since fire (interval of years). See Table SM 7 for a full description of the predictor variables. A) *Pinus halepensis*, B) *Quercus ilex,* C) *Pinus nigra*. R^2m corresponds to the Pseudo-R^2 (fixed effects) while R^2c corresponds 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.

storage (Santini et al., 2019), respectively. Finally, when populations are very close to the wet edge of the niche, *P. halepensis* would be prone to be replaced by other species which are more competitive under these conditions (e.g., *Quercus* spp.).

In the case of *Q. ilex*, burned populations experiencing climatic conditions in the post fire years far from the wet edge of the niche (both near the niche core or close to the dry edge) were more prone to experience a replacement by other species, likely due to a reduction of the growth of its 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 (Bussotti and 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 diminish *Q. ilex* dominance, which could be due to a better growth of other species (Supplementary material Table SM3). Locations with greater variability in the distance to the wet edge of the niche after the fire exhibited higher maintenance of *Q. ilex*, probably because this species has large reserves in its storage organs which buffer environmental variability (El Omari et al., 2003). Finally, greater severity of fires was associated with species dominance shift in burned *Q.ilex* populations, likely because high-intensity fires damage the bud bank or result in resprouts more sensitive to dry conditions than after low-intensity fires (Parra and Moreno, 2018).

For *P. nigra*, populations with mean pre-fire conditions far from the niche core were more likely to undergo a shift in species dominance after the fire, likely because under these conditions growth rates were low relative to other co-occurring species with more effective post-fire regenerative strategies (i.e., resprouting *Quercus* spp.). However, the occurrence of post-fire years near the wet edge of the niche promoted in some cases the maintenance of *P. nigra* as dominant species, probably due to a growth enhancement of the surviving trees. The post-fire replacement of *P. nigra* was higher under larger time lapses between the fire and the post-fire IFN3 sampling, likely reflecting delayed tree mortality. Finally, as expected in a fire-sensitive species, greater fire severity translated into important shifts in its dominance, because the high fire-induced mortality of adults is not balanced by the establishment of new seedlings.

Overall, this study shows that the species' climatic niche and the delineation of wet and dry niche edges help understanding short-term responses to fires. The differential post-fire response of the three studied species according to their location within the species' climatic niche may reveal their differential sensitivity to climate change. Future climates will affect fire regimes' properties that, in turn, could affect the effectiveness of reproductive and regenerative strategies, creating opportunities for colonization by other species after fire and thus promote sudden ecosystem shifts (Batllori et al., 2019). Although both *P. halepensis* and *Q. ilex* are adapted to fire in the Mediterranean Basin (Díaz-Delgado et al., 2002), our findings suggest that future extreme droughts may hinder *Q. ilex* regeneration more than that of *P. halepensis* (Barbeta et al., 2013), in spite of the recent mortality events observed in the latter (Valeriano et al., 2021).These differences in post-fire resilience highlight the importance of understanding how current and future conditions may displace populations from their historical positions within the climatic niche, or even push them beyond it. By computing bioclimatic variables from regional climate projections based on RCP scenarios (e.g., RCP4.5 representing moderate emissions and RCP8.5 representing high emissions; Berio Fortini et al., 2022; IPCC, 2023), the future position of populations relative to the species' climatic niche could be projected. This would serve to estimate potential post-fire recovery scores based on populations' distance to the wet and dry niche edges that, in the context of adapting forest management plans to the foreseen climatic conditions, may aid in determining the priority of required interventions (Mckenney et al., 2011) over the landscape. Moreover, 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 increase our understanding of ecosystem resilience into the future.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

N.J. Elvira reports financial support was provided by Spanish Government FPU grant 18/01037 and the associated grant for internships. F. Lloret reports financial support was provided by the Spanish Government PID2020–115264RB-I00 project. F. Lloret reports financial support was provided by Spanish Government TIPMED CGL2017–87176-P project. F. Lloret reports financial support was provided by the Generalitat of Catalonia Department of Education 2021-SGR 00849 grant. E. Batllori is a Serra Húnter fellow. The other authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123301.

Data availability

I have shared the link to my data at the Attach file step
IFN2 (MAPA)
IFN3 (MAPA)

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