Landsc Ecol (2025) 40:79
https://doi.org/10.1007/s10980-025-02093-1

RESEARCH ARTICLE

Biophysical drivers of *Pinus nigra subsp. salzmannii* post-fire regeneration: role of fire refugia

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Received: 14 January 2025 / Accepted: 4 April 2025 / Published online: 9 April 2025

Abstract

Context Recent shifts in fire regimes challenge recovery of forest ecosystems. In Catalonia, Spain, the capacity of *Pinus nigra* to persist has been affected by recent high severity fires.

Objectives To understand the biophysical conditions that support *P. nigra* recovery after high severity fire, we investigate the main biophysical drivers—seed availability, community interactions, water, and nutritional constraints—affecting post-fire regeneration patterns in Catalonia.

Methods We identified fire refugia and calculated the distance-weighted refugia density (DWD) across four fire footprints to represent the seed source abundance. We surveyed abundance of regeneration and shrub cover on 270 sites. We tested identical statistical models for "inside" and "outside" fire refugia, to assess the role of fire refugia and main biophysical drivers on post-fire regeneration.

Results The DWD had a positive effect on post-fire *P. nigra* recovery, with a stronger effect outside refugia than inside. Inside fire refugia, canopy trees had a sheltering effect on post-fire regeneration, reducing negative effects of heat load, particularly at higher aridity plots. Presence of *Rubus* spp. broadleaf shrubs enhanced the abundance of regeneration both inside and outside refugia. Total shrubs cover negatively impacted regeneration inside refugia and sites with greater aridity outside refugia but exerted a facilitative effect on *P. nigra* regeneration outside of fire refugia at sites with lower heat load.

Conclusions Seed source abundance is an integral driver of post-fire regeneration however, biophysical site conditions are important filters that amplify or diminish regeneration. This ecological information can be used to tailor post-fire management goals for forest recovery.

Keywords Fire refugia · Heat load index · Post-fire recovery · Pine forests · Vegetation dynamics

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-025-02093-1.

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Introduction

Wildland fire has shaped the dynamics of Mediterranean forest ecosystems for millennia, with species adaptation to regional fire regimes, which are characterized by their frequency, intensity, size, spatial pattern, season, and severity (Pausas 2004; Pausas and Keeley 2009; Ne'eman and Arianoutsou 2021). Most Mediterranean woody species exhibit some adaptation traits that typically ensure the persistence and recovery of forests after fires, either by reducing the probability of mortality of the adult trees (e.g. due to thick bark), or by enabling post-fire regeneration (e.g. due to resprouting capacity, serotinous cones, etc.) (Paula et al. 2009; Pausas 2019; Ne'eman and Arianoutsou 2021). For many non-serotinous conifer tree species, the dispersal of seeds from surviving trees or patches of trees after a fire – fire refugia –provides an important mechanism for landscape-scale fire resilience (Ordóñez et al. 2006; Christopoulou et al. 2014; Rodman et al. 2023).

In the last century, changes in both climate and vegetation have contributed to alterations of fire regimes across Mediterranean ecosystems (Stephens et al. 2013). The rise in temperatures, decreased precipitation, and extended fire seasons have contributed to increased fire frequency and severity in Mediterranean areas (Pausas 2004; Stephens et al. 2013). Moreover, Mediterranean Europe has undergone widespread land-use changes due to rural abandonment, which combined with forest reforestation programs and fire suppression policies resulted in increased stand densities and forest fuel connectivity at stand and landscape scales (Pausas and Keeley 2009; Moreira et al. 2011). The resulting increase in fire hazard and high severity fire effects is challenging the resilience of forest ecosystems, particularly for species whose adaptative mechanisms are not aligned with these new fire regimes (Lucas-Borja et al. 2017; Downing et al. 2019). This is an acute concern for non-serotinous obligate seeders whose post-fire recruitment is hindered by recent shifts in fire regimes, with examples around the world, including: *Pinus ponderosa* in the United States, *Pinus nigra subsp. nigra* in Greece and *Pinus nigra subsp. salzmannii* in Spain. These pine species have shown a decrease in post-fire regeneration after high severity fires and in the absence of tree planting, only re-establish in areas close to fire refugia, which act as seed source (Christopoulou et al. 2014; Martín-Alcón and Coll 2016; Chambers et al. 2016). There is widespread concern for post-fire recovery of these foundation species in dry forest settings.

The concern about post-fire recovery for *Pinus nigra subsp. salzmannii* (black pine, here after *P. nigra*)¸ is particularly highly die to current low levels of natural regeneration (Lucas Borja et al. 2021) and its inclusion in the European Union's endangered habitat list (Resolution 4/1996 in the Convention on the Conservation of European Wildlife and Natural habitats). *P. nigra* populations commonly grow on north facing slopes, where humidity levels are higher, and thrive best in nitrogen-rich soils (Regato and Del Rio 2009; Barčić et al. 2022). This pine exhibits low seed germination and seedling survival due to high rates of seed and seedling predation (Lucas-Borja et al. 2010), high sensitivity to temperature and moisture, and dependence on masting years for regeneration (Cerro Barja et al. 2009; Lucas-Borja and Vacchiano 2018; Lucas-Borja et al. 2021). Seedling establishment is more successful under intermediate canopy cover (50–80%) and can be facilitated by shrub species that provide shelter and protection in xeric sites (Tíscar 2003; Tíscar and Linares 2013). *P. nigra* exhibits traits that allows it to resist frequent low- and moderate-intensity surface fires, including thick bark, efficient self-pruning, and late-winter seed dispersal (Tíscar and Linares 2011; Morales-Molino et al. 2017). However, it is highly vulnerable to high-intensity crown fires, which have become more frequent in recent decades, leading to a reduction in the extent of *P. nigra* forests in Catalonia (Beltrán et al. 2018). These fires scorch and torch the leaves of the trees, killing the tree and consuming or damaging the cones and seeds, resulting in limited post-fire seed sources. Consequently, large portions of *P. nigra* forests have transformed to oak-dominated stands or shrublands (Retana et al. 2012; Martín-Alcón et al. 2015).

P. nigra can still regenerate after large and intense fires if seed sources are nearby, either from surviving trees – fire refugia – or from surrounding forests at, or outside, the fire perimeter (Gracia et al. 2002; Retana et al. 2002; Ordóñez et al. 2004, 2006). Several studies have highlighted seed source availability as a key factor in *P. nigra* regeneration, but they have mostly focused on one-dimensional distance measurements to the nearest seed source (Gracia et al. 2002;

Ordóñez et al. 2004; Christopoulou et al. 2014). In contrast, studies conducted in the United States have shown that one-dimensional distance metrics fail to account for total seed source availability (Coop et al. 2019). Accordingly, incorporating both one-dimensional distance measurements and a refugia density component—through abundance-weighted bidimensional metrics—into models improves explanatory power and better reflects the full spatial ecology of post-fire landscapes (Downing et al. 2019).

In addition to proximity to seed sources, the success of post-fire regeneration depends on factors acting at the site or community level. Microclimatic site conditions such as heat load, moisture deficit, soil fertility, and interactions with other species have proven important drivers of seedling regeneration for several species in the Western US (Downing et al. 2020). In the case of *P. nigra,* post-fire performance also depends on its ability to withstand competition for growing resources from other trees and shrubs or benefit from positive interactions with other species (Christopoulou et al. 2014; Martín-Alcón and Coll 2016). For example, Sánchez-Pinillos et al. (2018) demonstrated important growth reductions in post-fire regeneration of this pine due to competition for water from resprouting oak. Meanwhile, Christopoulou et al. (2014) found that the presence of ferns positively impacted the density of post-fire black pine recruitment in a study conducted in Southern Greece. Yet, the persistence of fire refugia remains a key component in the success of post-fire regeneration (Davis et al. 2019; Zellweger et al. 2020), and the interactions between refugia, their structure and environmental controls (e.g. climate, competition) can modulate the regeneration capacity of non-serotinous pine species such as *P. nigra* (Downing et al. 2019; Busby and Holz 2022; Davis et al. 2023).

Most studies of post-fire regeneration in dry forest areas have been conducted at reduced scales, often focusing on experimental setups or a limited number of drivers (Retana et al. 2002; Ordóñez et al. 2006; Lucas-Borja et al. 2017). There is a notable scarcity of research that integrates various potential drivers of post-fire regeneration across different spatial and temporal scales. An exception to this are some studies conducted on *Pinus ponderosa* in the United States, which have provided a more integrative comprehension of the roles of various factors and their interactions in modulating post-fire regeneration for this non-serotinous tree species that shares similar fire adaptive traits to *P. nigra* (Downing et al. 2019). Accordingly, our research aims to provide an integrative study of the biophysical factors affecting post-fire regeneration patterns of non-serotinous European Mediterranean dry forest pines, using *P. nigra* in central Catalonia (Spain) as a representative species. We tested hypotheses related to landscape-level factors, including seed source availability, topographic setting, and climate; as well as community-level or microsite factors, such as plant community interactions and fertility indicators, to assess the conditions supporting *P. nigra* regeneration in the context of increased wildfire severity across the region.

We hypothesize that if seed availability is the primary limiting factor, (i) landscapes with more abundant *P. nigra* fire refugia will exhibit higher post-fire recruitment, and (ii) an abundance-weighted metric of fire refugia density will outperform simpler metrics, such as distance to nearest seed source. Additionally, we hypothesize that (iii) if water and nutrient stress – rather than seed availability – constrain *P. nigra* regeneration, seedling abundance will vary at the microsite level, depending on site conditions and plant community composition. Lastly, (iv) we anticipate facilitative interactions between *P. nigra* and other species, though these interactions may vary with topographic conditions. The results of our study will contribute to the stewardship of *P. nigra* in Mediterranean ecosystems by illustrating the conditions under which this species can persist despite the challenges posed by wildfires and climate change.

Methods

Study area

The study was conducted in areas affected by wildfires that impacted *P. nigra* subsp. *salzmannii* (black pine) populations in Catalonia (NE Spain). The native range of *P. nigra* includes the south of France to the southeast of Spain, where it represents 4.7% of total forest cover in Spain (Vacek et al. 2023). In Catalonia, *P. nigra* naturally grows in the Pre-Pyrenees, the Pre-coastal Range, and the Southeastern Iberian System, covering approximately 140,000 hectares and approximately 10% of the total forest cover (Beltrán et al. 2018). The range extends between 500 and

1600 m of elevation, in a transition area between high mountains and Mediterranean xeric lowlands. Black pine prefers calcareous deep soil and humid sites, mainly facing the northern aspects and is sensitive to drought and high intensity fires (Morales-Molino et al. 2017; Vacek et al. 2023).

In this study, we examined the post-fire recovery of *P. nigra* after stand-replacing, high-severity fires. These fires occurred in the Pre-Pyrenes and the Pre-coastal Range, spanning a gradient of climatic and topographic conditions (annual precipitation: 480–750 mm; mean annual temperature: 13–16 °C; elevation: 370–910 m). The final selection consisted of four fires that occurred between 1994 and 2003 in Central Catalonia, where most of this pine's population is found. The fires we chose were: Montmajor (burned in 1994), Pontils (1994), Solsonès (1998) and Sant Llorenç (2003). Measurements of post-fire recovery were collected in 2023, representing the young stages of forest recovery and succession. These four fires represent 84.56% of the total burned area for the distribution of *P. nigra* in the last three decades (Fig. 1).

The Solsonès and Montmajor fires occurred in the Pre-Pyrenees region and are the largest fires recorded in *P. nigra* forest ecosystems in recent decades, each burning more than 20,000 hectares (Fig. 1 and Table 1). Both fires covered varied landscape conditions, including mountain terrain, valleys, and plains; with a high variability in elevation (> 400 m range; Table 1). In contrast, the Pontils and Sant Llorenç fires are located in the Pre-Coastal Range, at the lower limit of *P. nigra* distribution in Catalonia (Fig. 1). Pontils is the smallest selected fire (261 ha), affecting an area between 560 and 780 m in elevation next to an open pit mine, with steep slopes and interspersed with agriculture and livestock fields. The Sant Llorenç fire occurred within a protected natural area with elevations ranging from 470 to 740 m and is the most recent fire from the ones we studied.

In the Solsonès, Montmajor and Pontils fire footprints the post-fire landscape is characterized by a combination of fire refugia and burned areas across, forests and agricultural landscape, contributing to a high landscape heterogeneity. For all these fires, more than a third of the burned areas are covered by non-forested lands. For the Montmajor and Solsonès fires, less than 15% of the remaining forest cover is *P. nigra*, while in Pontils it represents up to 18.8% of the remaining forest cover (Table 1). The mountainous area where the Sant Llorenç fire burned has few valleys and low landscape heterogeneity (only 3.8% of non-forested lands) (Table 1). Most of the remaining forests are mixed conifer and broadleaf stands; with 14.1% of the remaining forest cover corresponding to *P. nigra* stands.

Identifying fire refugia

Fire refugia were quantified following Downing et al. (2019), Walker et al. (2019) and Coop et al. (2019). First, we gathered fire perimeters defined by the firefighters' services of the Catalan government (Generalitat de Catalunya 2024). Then for each fire we created a mosaic of orthoimages from the Spanish National Orthophoto Program (PNOA) with a spatial resolution of 0.25×0.25 m. We identified unburned patches using the orthoimages from five to seven years after each fire, selected to avoid under- or over estimation of seed sources/trees due to second-order fire effects (e.g., delayed mortality or canopy recovery). We performed a binary supervised classification of the images, selecting at least 200 points as training sample for the classification ($n > 100$ points per class), and visually identifying them as forest (1) and non-forest (0) areas. We then used a support vector machine (SVM) algorithm implemented in the R package *caret* (Kuhn 2007) to classify the image mosaics based on the characteristics of the training sample, obtaining a raster with two classes: forest (1) and non-forest (0). This was done using a radial kernel, due to its high performance in classification assessments (Liu et al. 2017). Additionally, the sigma (values ranging from 0.001 to 1) and Cost (ranging from 1 to 700) hyperparameters were tuned using a tenfold cross validation with 5 repetitions. The classification output presented an overall mean accuracy of 0.8749 and a mean kappa of 0.7497. The results were resampled to a working spatial resolution of 2×2 m using the nearest neighbor approach.

To exclude potential misclassifications for shrublands and woody crops as fire refugia – because of their similarity in spectral and spatial properties – we filtered the SVM classification results using information on canopy height from Airborne Laser Scanning (ALS) data provided by the Spanish Geographic Institute as part of the PNOA flight campaign (PNOA-CNIG 2024). The PNOA airbone-LiDAR data, flown

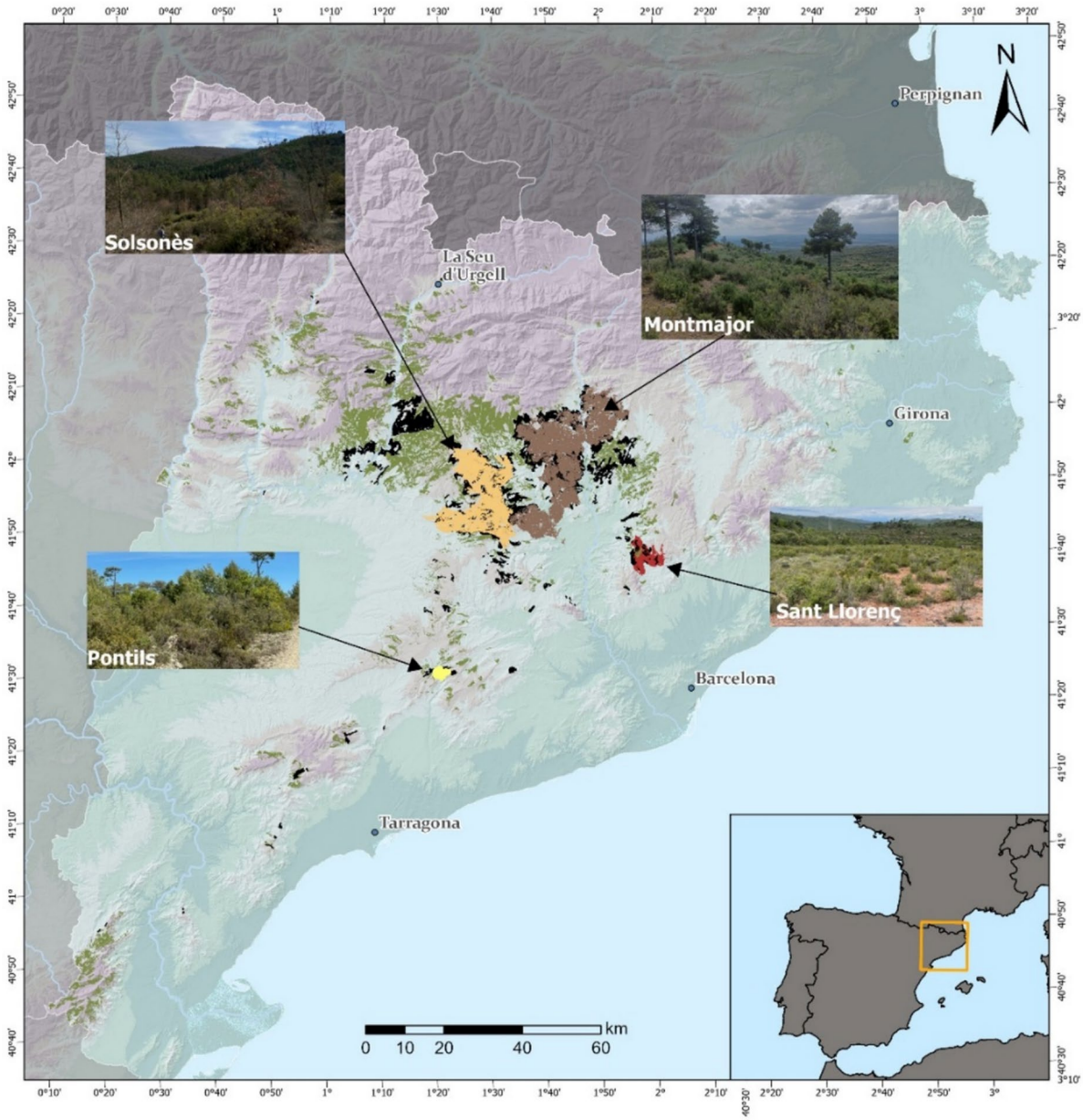

Fig. 1 Location of the studied fires in Catalonia. Green shading indicates the current distribution of *P. nigra*, whereas black polygons represent areas of *P. nigra* that were affected by wildfires in the study period. The perimeter of the four selected fires is indicated in different colors, along with a representative picture of each study site: Solsonès, Montmajor, Pontils and Sant Llorenç

in 2016 has a nominal point density of 0.5 points/m^2 in the study area, with a vertical accuracy of ± 0.2 m and a horizontal accuracy of ≤ 0.3 m. We calculated the maximum canopy height in 2×2 m resolution rasters, using the *pixel_metrics* function of the *lidR* R package (Roussel et al. 2020; Roussel and Auty 2024). Only pixels with a maximum height (H_{max}) of more than 5 m were kept as unburned forests. This threshold allowed us to differentiate between shrubs and trees, while ensuring that post-fire pine regeneration was not misclassified as unburned vegetation. The outcome of this process was a new raster with a

Table 1 Description of study fires, including year of fire, total burned area, burned area corresponding to *P. nigra* forests and non-forested areas, the percentage of area covered by *P. nigra* burned at different severities, number of plots per fire and the sampled elevation gradient

Fire	Year	Burned area (ha)			*P. nigra* burned for each severity class[1] (%)				Plots	
		Total	Non forest	*P. nigra*	Unburned (< 105)	Low (105–200)	Medium (200–355)	High (> 355)	Number of sampled plots	Elevation (m)
Pontils	1994	261.1	174.9	56.3	2.0	5.6	57.2	35.2	25	560–780 (681)
Montmajor	1994	38,963.9	16,670.9	7048.9	8.1	16.8	41.4	33.7	94	370–860 (601)
Solsonès	1998	23,940.3	9757.7	10,370.8	0.8	2.0	10.9	86.3	111	470–910 (680)
Sant Llorenç	2003	4333.6	951.2	366.7	0.8	2.9	15.8	80.5	40	470–740 (606)

For elevation minimum, maximum and mean (in parentheses) values are provided. For fire severity the ranges of the RBR index[1] used to define each class are indicated in parenthesis

[1]The severity classes were calculated using the Relativized Burned Ratio Index (RBR) (Fernández-Guisuraga et al. 2023)

better classification of unburned forest (1) and non-forest (0).

To optimize computational processing, we applied a 3 × 3 cell majority focal filter to the previous raster, excluding some of the isolated trees from our classification. This reduced the potential noise coming from single-pixel patches, allowing a robust aggregation into refugia while preserving most of the smallest forested patches. We converted the pixels into polygons to aggregate them, following Downing et al. (2019). Polygons within 20 m from each other were considered as a single polygon; and gaps smaller than 50m^2 within the polygons were merged into the surrounding polygon. This process resulted in a map with all fire refugia for each fire footprint. To narrow our quantification of fire refugia to *P. nigra,* we intersected our refugia map with the Third Spanish Forest Map (MITECO 1997) and kept only the refugia corresponding to post-fire stands dominated by *P. nigra.* The Forest Map provides information at a 1:25,000 scale, identifying the three dominant species in each forested area and was created using image analysis and field validation.

Seed source density mapping

The *P. nigra* refugia maps were used to calculate the distance-weighted refugia density (DWD) across the landscape. We created a 120 × 120 m moving window calculation, adjusted to account for *P. nigra*'s seed dispersal distance and seedling recruitment rates. We used a 60 m distance from the central pixel (i.e., 120 m side of the moving window), as studies have shown that the number of seedlings found beyond this distance from a seed source are very low (Christopoulou et al. 2014). For the central pixel of the moving window, we calculated the amount and location of fire refugia within the 120 × 120 area using a two-dimensional distance-weighted kernel, formulated as:

$$\mathrm{DWD} = \sum_{i=1}^{N} \frac{1}{(d_i + 1)} \quad (1)$$

where d_i represents the distance between each forested pixel inside a moving window and the central pixel. This metric accounts for the exponential decrease in seed dispersal and regeneration with increased distance from seed source. The resulting surface reflects the major contribution of nearby seed sources, while weighing the importance of more distant seed sources. As a result, we produced a map with a continuous metric of two-dimensional refugia density ranging from a value of 0 in areas with no fire refugia, to a value of 193 in areas saturated with fire refugia.

Sampling design and fieldwork

Our field sampling campaign occurred between January and June of 2023. We selected field sampling locations by generating a set of random points, stratified based on the DWD gradient. We created a categorical version of the DWD map by dividing the values into quartiles. For each fire, we randomly located the same number of sampling points per class, ensuring a minimum distance between points of at least

100 m, to guarantee the independence of our sampling points. This distance corresponded to the maximum dispersion distance for *P. nigra* (Ordoñez et al. 2006). The number of plots per fire varied according to the fire area and landscape heterogeneity, so the largest fires had more sampling points than the smaller ones. We used an accumulation curve – abundance of *P. nigra* regeneration and number of plots – to ensure the proper sampling effort according to the heterogeneity of the fires; therefore, the Solsonès fire had more sampling points than Montmajor.

All potential sample points were assessed in the field, where some were excluded based on accessibility and the absence of *P. nigra* dominance within fire refugia. After screening, we sampled a total of 111 plots in the Solsonès fire, 94 in Montmajor, 40 in Sant Llorenç and 25 in Pontils (Table 1), for a total of 270 plots. At each site we established a 5-m-radius circular plot, measuring the abundance and height of *P. nigra* saplings and seedlings. We gathered information on species composition, mean height, and percentage cover of all shrubs and other tree species. From the center of the plot, we used a 0.5×0.5 m grid to take four measurements of total cover of shrubs, herbs, deadwood, stones, litter, and bare soil (Supplementary Fig. 1). In plots located within fire refugia, we measured forest stand variables, including tree stem density, basal area, and mean tree height.

Climatic and topographic data

We characterized each plot on topo-climatic conditions. We obtained the slope, aspect, and elevation for each plot by intersecting our sampling points with the Digital Terrain Models (DTM) of the Cartographical and Geological Institute of Catalonia, resampled to 30 m resolution (ICGC 2020). We also gathered daily records of minimum, maximum and mean temperature, as well as precipitation for the period 1994–2022, from weather stations of the Spanish Bureau of Meteorology (AEMET) and the Meteorological Service of Catalonia (METEOCAT). We used the *meteoland* R package (version 2.2.1, (De Cáceres et al. 2023), to interpolate the daily climatic values for each plot, considering geographical position, slope, elevation, and aspect. We summarized the climate data by year, and we calculated the average annual values for the period from the year of the fire to 2023 (field sampling year). We calculated the heat load index (HLI), as a proxy for aridity, using the *SpatialEco* package in R (Evans et al. 2023). This index ranges from 0 (coolest) to 1 (hottest) and uses topographical parameters of aspect and slope to estimate heat differences between aspects. It applies McCune's (2007) equations, assigning the lowest values to the northeast-facing slopes and the highest to the southwest-facing slopes; southeast slopes typically have lower temperatures compared to their southwest counterparts under equivalent radiation (Evans et al. 2023).

Data analysis

To assess the biophysical drivers of *Pinus nigra* post-fire regeneration, we selected explanatory variables representing key ecological factors known to influence seedling establishment and survival. To test our two first hypotheses related to fire refugia as seed source, we compared the predictive capacity of two indicators of seed source availability: Euclidean Distance to the nearest seed source and distance-weighted refugia density (DWD). Euclidean Distance has been commonly used to explain *P. nigra* post-fire regeneration in the Mediterranean Basin (Ordóñez et al. 2006), whereas DWD, which integrates both seed source abundance and spatial configuration, has proven to be a good predictor in conifer forests of the United States (Downing et al. 2019). We evaluated the predictive capacity of both variables using univariate models, and the best-performing predictor was then used as the seed source availability indicator for building the remaining models.

We then selected a set of potential variables impacting *Pinus nigra* post-fire regeneration based on three main criteria: ecological significance, statistical performance in exploratory analyses, and avoidance of multicollinearity. To test for collinearity among candidate variables, we calculated Pearson correlation coefficients. When the two variables were strongly correlated ($|r| > 0.7$), we retained only the one with stronger ecological relevance. Topographic effects of the plot were represented by the Heat Load Index (HLI), which quantifies topographically induced aridity—a factor previously linked to *P. nigra* post-fire regeneration in a section of the Solsonès fire (Gracia et al. 2002). We also included mean annual precipitation since the fire, given its influence on pine masting, germination, and growth (Lucas-Borja et al.

2016; Lucas-Borja and Vacchiano 2018). During exploratory analysis, Principal Component Analysis (PCA) revealed that *Rubus* spp. grouped separately from other shrub species, reinforcing its role as a distinct ecological factor associated with fertility (Walter et al. 2016). In contrast, total shrub cover was included as a broader indicator of facilitative or competitive effects, as shrubs have been shown to facilitate *P. nigra* seedling growth in unburned stands (Tíscar 2003; Tíscar and Linares 2013). Finally, we incorporated the interaction between total shrub cover and HLI, considering that aridity has been shown to influence facilitation trends in unburned sites (Tíscar and Linares 2013; Lucas-Borja et al. 2016).

To test the effect of fire refugia on *P. nigra* regeneration, we built two identical models: one including sample plots located inside fire refugia and another including plots outside refugia. Both models were developed using the *glmmTMB* function from the *glmmTMB* package in R. Each model incorporated the previously selected predictors: seed source availability, total shrub cover, *Rubus* spp. cover, Heat Load Index, and precipitation to evaluate their influence on *P. nigra* abundance. To determine the most appropriate statistical modelling approach, we tested each subset of the data –inside and outside refugia– for overdispersion and zero-inflation using the DARHMA R package (Hartig 2022) and assessed spatial autocorrelation with the *gstat* R package (Pebesma 2004). These tests confirmed that our data was zero-inflated and over dispersed, while spatial autocorrelation was not a concern (Supplementary Fig. 2).

We used a zero-inflated negative binomial model to test our hypotheses statistically. To enable a direct comparison of variable effects inside and outside refugia, we used identical variables in the conditional part of both models. However, in the zero-inflation component, we used different variables to represent seed source availability while maintaining their biological relevance in each context. Inside refugia, we selected basal area as the zero-inflation variable as lower basal area values—associated with younger stands or large canopy openings—could explain the absence of regeneration due to reduced seed availability. Outside refugia, we used the density of the surrounding refugia (DWD), assuming that limited regeneration could be linked to both the distance to refugia and the number of seed sources in the landscape. We also tested random effects associated with fire identity in both models (inside and outside refugia) to account for variability not explained by fixed effects. Model performance was assessed by comparing the zero-inflated negative binomial with a mixed-effects version using the Akaike Information Criterion (AIC). We verified that all models met the assumptions of normality and heteroscedasticity using the *DARHMA* package in R (Hartig 2022).

The sign and magnitude of parameter estimates were used to assess the effects of the predictors, indicating whether they promoted (positive effect) or limited (negative effect) *P. nigra*'s post-fire regeneration. We used the *p-value* to determine statistical significance. We analyzed the interaction between HLI and shrub cover by assessing the effect of heat load on *P. nigra* regeneration for different shrub cover levels (5th, 50th and 95th percentile). To evaluate the role of fire refugia in post-fire regeneration, we compared the effect of all variables between models. This was possible since both models – inside and outside refugia – had the same model formulation. We evaluated the relative importance of each predictor by comparing the AIC of the full model – which included all predictors – against models in which each variable or interaction was removed. A decrease in model performance (i.e., an increase in AIC) when removing a variable indicated strong support for that predictor as a key driver of seedling abundance. Conversely, if removing a variable led to a lower AIC ($\Delta AIC > 0$), this suggested that excluding the variable improved model performance, indicating its limited relevance in explaining post-fire regeneration.

Results

Less than 20% of the pre-fire *P. nigra* forests remained as fire refugia inside the four study fire perimeters. The greatest loss of *P. nigra* forests occurred in Solsonès and Sant Llorenç fire footprints with less than 5% remaining as post-fire refugia (615.35 ha and 34.32 ha respectively), while the smallest loss was in Montmajor, where approximately 15% of the original *P. nigra* forests remained as fire refugia (2983.70 ha). In all fires, fire refugia consisted of small patches with both mean and median areas of less than one hectare, and were primarily located around the fire's perimeter (Fig. 2).

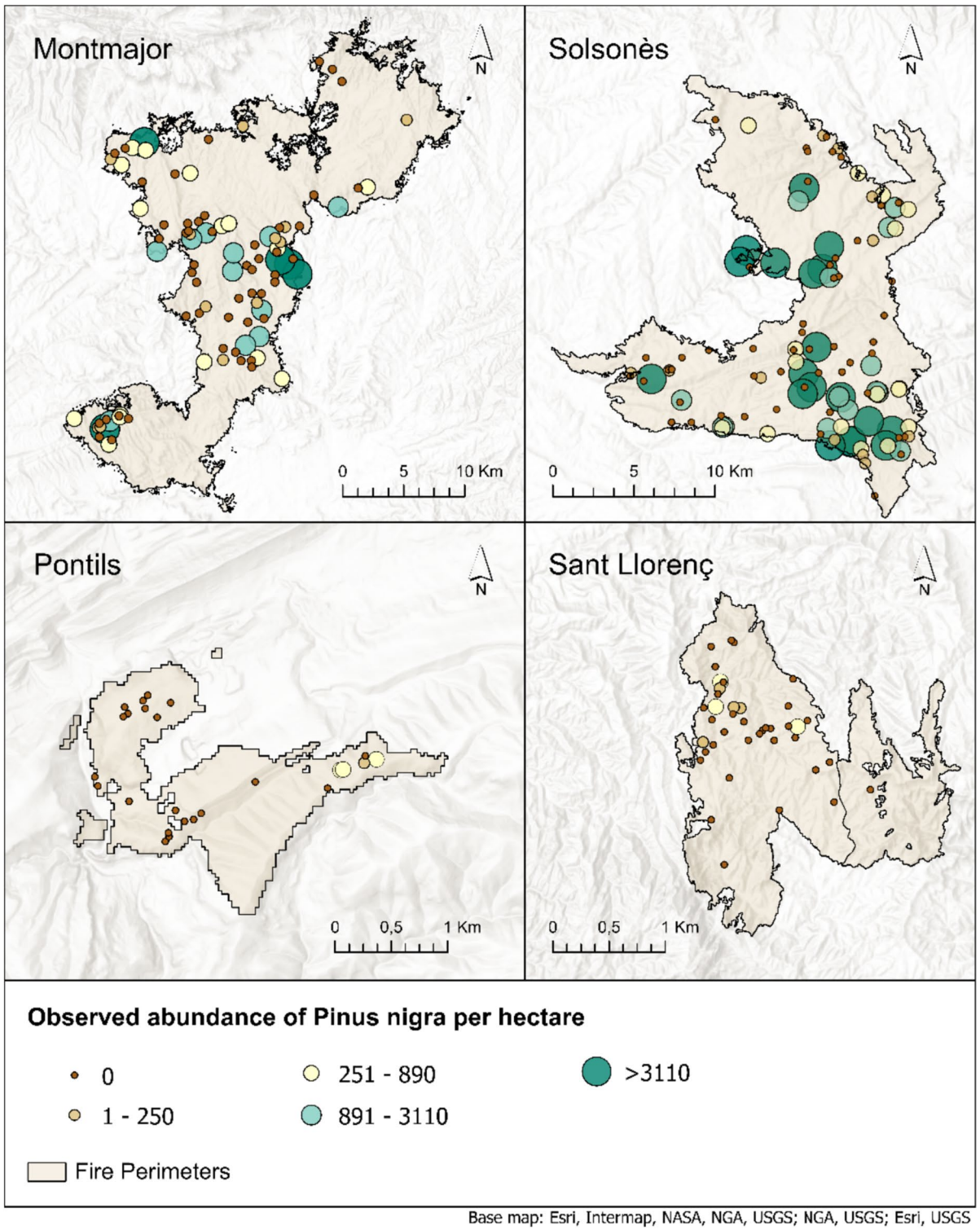

Fig. 2 Spatial distribution in the level of *Pinus nigra* regeneration in the four study fires in Catalonia, Spain. Green larger circles indicate a higher number of juvenile pines (seedlings and saplings) per hectare, while dark brown-small circles identify sites with no regeneration of this species

Fires located in the Pre-Pyrenees Range showed much higher regeneration levels than fires in the Pre-Coastal Range. In Pontils and Sant Llorenç, less than a quarter of the sampling sites exhibited some *P. nigra* regeneration (16% and 17.5%, respectively), while roughly one half of sampling sites in Montmajor (46.8%) and Solsonès (54.1%) supported regeneration. However, the abundance of regeneration was highly variable among plots in all fires, particularly in Montmajor and Solsonès (Fig. 2). This high variability in abundance was observed both outside (0 to 25,974 pines/ha) and inside refugia (0 to 13,242 pines/ha). Outside refugia, more than half of the plots (63.2%) recorded no seedlings or saplings. Mid-to-high levels of regeneration (> 890 pines/ha; see Fig. 2) occurred in 15.5% of the plots. Inside refugia the regeneration abundance was slightly higher, with only 47.4% of the plots lacking regeneration and 18.9% having mid-to-high numbers (> 890 pines/ha) of *P. nigra* seedlings and saplings.

Shrub cover was similar inside and outside refugia, with a mean cover of 60% and 70%, respectively (Fig. 3A). Species richness included 42 species detected inside refugia to 50 species outside, with an almost identical composition in both cases. Rosemary (*Salvia rosmarinus*) was the most dominant and frequent shrub species both inside (32.7% dominance and 13.5% frequency) and outside refugia (35.3% dominance and 14.2% frequency), followed by *Quercus coccifera, Genista scorpius* and *Rubus* spp. *Rubus* spp. were the second most frequent and

Fig. 3 Photos of selected sample plots showing post-fire regeneration of *Pinus nigra* (white circle) and other woody species (arrows). **A** *P. nigra* regenerating alongside various shrub species, including *Quercus coccifera* and *Genista scorpius* (blue arrows). **B** *P. nigra* co-occurring with *Rubus spp.* (yellow arrows)

dominant species inside refugia and the fourth outside (Fig. 3B; Supplementary Table 2).

According to the fitted models, the zero-inflated negative binomial was the best fit to our data, as the mixed model did not improve the model's performance, and the variance of the random variable was not different from 0. We selected DWD as the indicator for seed source availability, as univariate models found that DWD was a stronger predictor than the Euclidean Distance to the closest seed source (ΔAIC = −3.8 outside refugia and −4.3 inside refugia), supporting our second hypothesis (Supplementary Table 1).

P. nigra regeneration outside and inside of fire refugia showed differences in biophysical drivers of abundance, estimated using the conditional components of the models. For the model outside of refugia, all tested variables significantly explained post-fire *P. nigra* regeneration (p-value < 0.05, Table 2). Inside refugia, regeneration abundance was significantly related only to *Rubus* spp. cover (p-value: 0.014) and precipitation (p-value: 0.006). *Rubus* spp. cover had a positive effect on *P. nigra* regeneration both inside and outside refugia (Fig. 4A) and was one of the strongest predictors of regeneration abundance (ΔAIC −5.2 and −7.2, respectively, Table 3). The density of refugia (DWD) also had a positive effect on regeneration (Fig. 4B). Outside refugia, increasing DWD from the 25th to 75th percentile let to a 10.8% increase in *P. nigra* regeneration (Table 2), while inside refugia the increase was lower (7.8%). The DWD variable was only significant outside refugia (p-value = 0.013 *vs.* p-value = 0.164 inside, Table 2), where it had the second lowest explanatory power of all variables considered, while inside refugia, it had the lowest (ΔAIC = −4.3 and −0.3, respectively; Table 3). Since DWD was included in both the conditional and zero-inflation components of the outside refugia model, part of its explanatory power may be captured in the zero-inflation component, reducing its effect in the conditional part (Table 2).

Within the range of *P. nigra* sampled with our field plots, precipitation had a negative effect on *P. nigra* regeneration abundance both inside and outside refugia, with the highest post-fire regeneration occurring at annual rainfall levels around 500 mm (Fig. 4D, Table 2). Although precipitation was a significant predictor in both models, it played a more important role in explaining the level of regeneration inside refugia (ΔAIC = −6.9), whereas outside refugia it had the lowest explanatory power of all predictors (ΔAIC = −2.9, Table 3).

Table 2 Parameter estimates, confidence intervals, and p-values for the zero-inflated negative binomial GLMM explaining the abundance of *P. nigra* regeneration after fire in areas outside and inside fire refugia

Variable	Full model: outside fire refugia				Full model: inside fire refugia			
	Estimate	Confidence intervals		p-value	Estimate	Confidence intervals		p-value
		Min	Max			Min	Max	
Conditional								
Intercept	10.790	6.730	14.849	0.000	13.899	7.796	20.003	0.000
DWD	0.013	0.004	0.021	**0.013**	0.005	−0.001	0.011	0.164
Heat load index (HLI)	2.731	−1.329	6.790	0.269	1.762	−3.836	7.360	0.605
Precipitation	−0.009	−0.016	−0.002	**0.034**	−0.014	−0.022	−0.006	**0.006**
Total shrub cover	0.043	0.002	0.084	0.082	0.001	−0.063	0.065	0.987
Rubus spp. cover	0.029	0.013	0.045	**0.003**	0.027	0.009	0.045	**0.014**
HLI: Total shrub cover	−0.090	−0.146	−0.034	**0.009**	−0.024	−0.107	0.058	0.627
Zero-inflation								
Intercept	1.476	1.067	1.884	0.000	0.542	−0.078	1.162	0.150
DWD	−0.026	−0.034	−0.018	0.000	–			
Basal area	–				−0.079	−0.144	−0.015	0.043

The conditional component specifies the model for the mean *P. nigra* seedling abundance holding the random effects constant, whereas the zero-inflation component accounts for the excess zeros beyond those expected under a negative binomial distribution. Statistically significant variables in each model are shown in bold

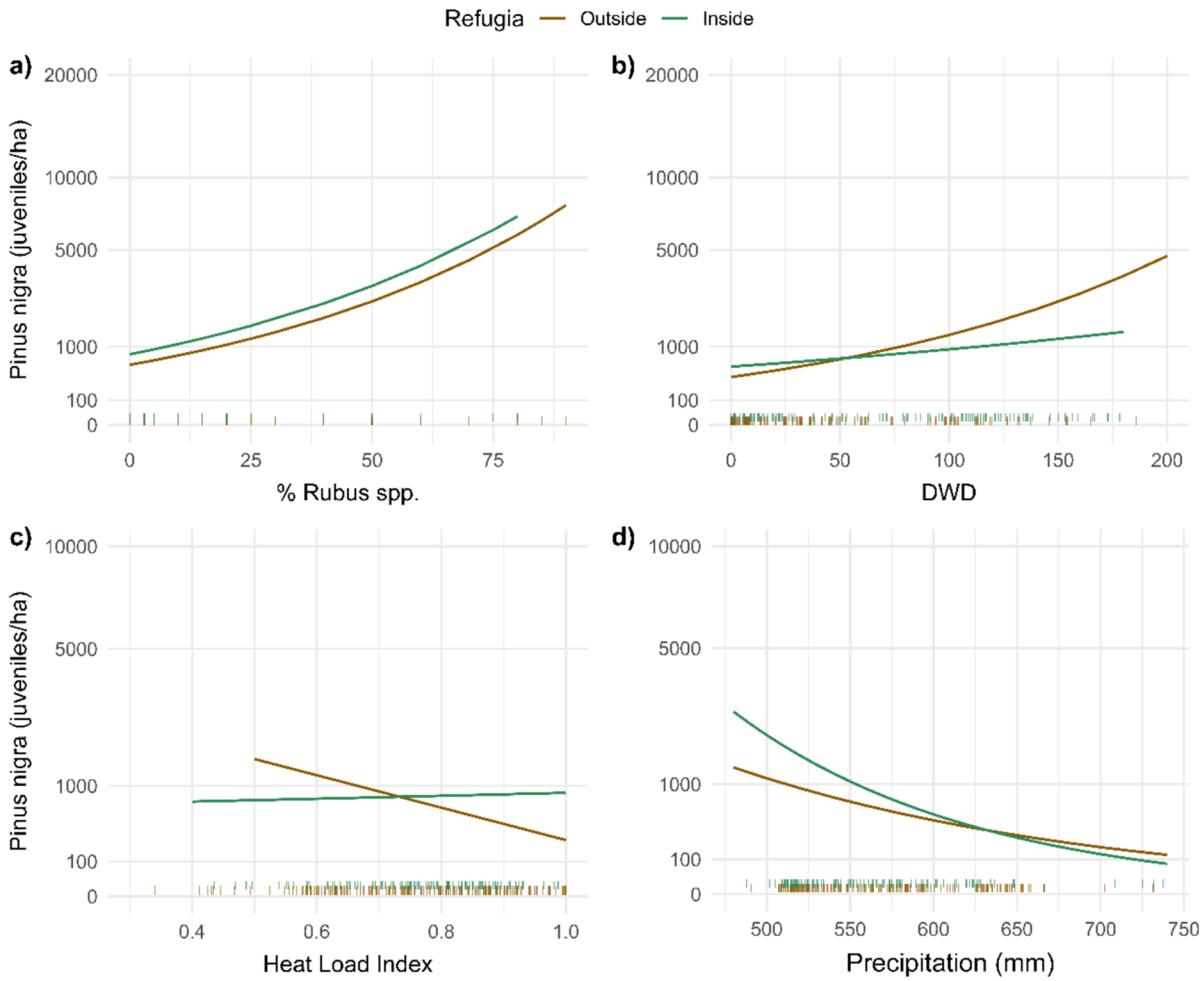

Fig. 4 Model parameters effect on the inferred abundance of P. nigra regeneration inside (green) and outside (brown) the refugia. The vertical lines at the bottom of all graphs represent the distribution of the observed values of the variable on the x axis. **a** Shows the effect of the cover of Rubus spp. **b** Presents the effect of the distance refugia density (DWD). **c** Indicates the effect of the heat load index. **d** Displays the effect of precipitation

Inside fire refugia, the heat load index and its interaction with shrub cover were not significant and did not explain regeneration abundance. Removal of these terms improved model performance (ΔAIC = 3.7 and 1.8, respectively; Table 3). However, to maintain the comparability between models for inside and outside refugia both variables were retained. This approach allowed us to assess the influence of fire refugia (i.e., forest cover) on how biophysical predictors affect *P. nigra* post-fire regeneration. Our results indicate that HLI influenced *P. nigra* regeneration differently inside and outside refugia (Fig. 4C, Table 2). Inside refugia, the level of regeneration remained constant across the HLI gradient, suggesting that aridity does not affect *P. nigra* recovery under canopy cover. However, outside of fire refugia, the increasing HLI caused a linear decrease in the abundance of *P. nigra*, as one of the most important predictors in the model (ΔAIC = −7.3, Table 3).

Shrub cover was the most important variable explaining *P. nigra* regeneration outside of the fire refugia (ΔAIC = −11, Table 3). Part of this biotic effect was related to an interaction with HLI (ΔAIC = −5), as the influence of HLI varied depending on shrub cover. At sites with low shrub cover, higher HLI values were associated with higher levels

Table 3 Variable importance inside the conditional part of the models explaining *P. nigra* regeneration abundance after fires in areas outside and inside fire refugia

Variable	Model outside fire refugia		Model inside fire refugia	
	AIC	ΔAIC	AIC	ΔAIC
Conditional				
Full Model	1296.9	0	960.7	0
Rubus spp. cover	**1304.1**	**−7.2**	**965.9**	**−5.2**
DWD	1301.2	−4.3	961.0	−0.3
Precipitation	1299.8	−2.9	**967.6**	**−6.9**
Total shrub cover [a]	**1307.9**	**−11**	**966.5**	**−5.8**
Heat Load Index (HLI)[a]	**1304.2**	**−7.3**	957.0	3.7
HLI: Total shrub cover	1301.9	−5	958.9	1.8

Variable importance was assessed by removing each variable from the conditional part of the full model and calculating the corresponding ΔAIC, which indicates the variable's relative contribution to model performance. Higher ΔAIC values denote greater explanatory power. Variables with a higher weight in explaining regeneration abundance for each model are shown in bold

[a]The effect of the ΔAIC models without either of the parameters in the interaction, also represents the effect of losing the interaction

of *P. nigra* abundance, whereas for mid to high shrub cover, the effect of HLI was negative (Fig. 5). Accordingly, shrub cover had a positive effect on post-fire *P. nigra* regeneration when HLI was below 0.5.

Within refugia, shrub cover was the second most important predictor of *P. nigra* regeneration, negatively affecting the species' abundance (ΔAIC = −5.8, Table 3). However, this effect was only significant (*p-value* < 0.05) in the best-fitting version of the inside refugia model, which excluded the HLI and interaction variables that reduced the model performance (Supplementary Table 3). This result is consistent with the ΔAIC values in the full model (Table 3), where removing shrub cover (and thus the interaction effect) improved the model performance. However, as we retained a less optimal version of the inside refugia model – including both HLI and the interaction – the negative effect of the shrub cover effect was not significant (*p-value* > 0.05), due suboptimal model performance (Table 2).

Discussion

Our study reveals a great variability in *P. nigra* regeneration abundance across the burned areas in

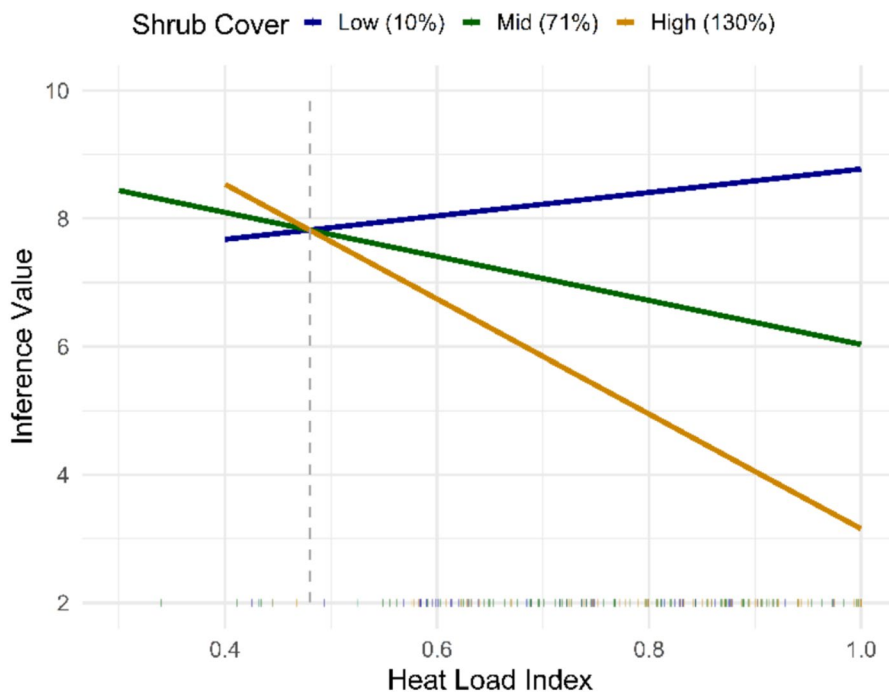

Fig. 5 Heat Load Index (HLI) interaction with shrub cover outside of fire refugia. The *x* axis represents observed values of shrub cover. The dashed line shows the inflection point of the trend lines; to its left in more benign conditions, shrubs have a positive effect on the abundance of the pine, while to its right in more extreme conditions this facilitation effect is lost

Catalonia, Spain, both inside and outside fire refugia. Our analysis suggests that microsite conditions strongly influence post-fire regeneration, after accounting for seed availability and seed dispersal. Our models indicate that factors such as the heat load (HLI), refugia presence, and shrub cover significantly shape post-fire forest recovery, in areas with sufficient seed availability. However, the magnitude and nature of these biophysical effects differed inside and outside refugia, where the sheltering influence of both overstory and understory vegetation affected *P. nigra* regeneration patterns.

Influence of landscape level drivers on the level of regeneration

Landscape context and the abundance of seed sources are crucial for *P. nigra* regeneration outside fire refugia. In our study, multi-dimensional measurements of refugia density – characterized via DWD – had a positive effect on regeneration levels. Our findings support previous work in the USA for ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*) and other non-serotinous conifers, where higher DWD levels are associated with increased post-fire regeneration (Downing et al. 2019; Coop et al. 2019). In post-fire conditions, distance to the seed source (i.e. to the nearest surviving tree) is a variable that has been broadly considered as the most important factor explaining post-fire regeneration of *P. nigra* var. *nigra* in Greece (Christopoulou et al. 2014) and *P. nigra* var. *salzmanii* in Catalonia (Martín-Alcón and Coll 2016). Our results suggest that DWD is an improved predictor of seedling abundance, highlighting the importance of accounting for a broader spatial ecology of the post-fire landscape when assessing the resilience of *P. nigra* to stand-replacing wildfires.

Existing studies of *Pinus nigra* have attributed regeneration levels to proximity to the seed source as the primary driver of spatial pattern (Ordóñez et al. 2004). While seed source certainly is the most important ecological factor required for regeneration, our study illustrates a strong ecological filter from microsite conditions, both inside and outside refugia. However, we highlight that our zero-inflation models consist of two components: the zero-inflated section and the conditional section. For the model of regeneration outside fire refugia, where we expect seeds source limitations to be strongest, DWD was included in both components: as the zero-inflation variable and as a predictor in the conditional model. Consequently, part of DWD's explanatory power was allocated to the zero-inflation section, potentially compartmentalizing its effect. Notionally, the zero-inflated component of the models represent a sub-population of the field sites with no regeneration because fire refugia are limited or absent, whereas the conditional component of the model aims to quantify how variability in fire refugia and other biophysical factors further affects regeneration. We suggest this compartmentalization does not affect our conclusions regarding the strong role of microsite variables in shaping regeneration (Lucas-Borja et al. 2017; Sánchez-Pinillos et al. 2018).

The importance of microsite conditions in *P. nigra* regeneration levels aligns with previous studies conducted for this species in Catalonia, where establishment after fires depended not only on the spatial distribution of seed sources but also on local aridity (Gracia et al. 2002). Similar results were also found in conifer forests of the Rocky Mountains, USA, where site temperatures regulated regeneration or survival regardless of the proximity to the seed source (Kemp et al. 2019). The strength of microsite influence on regeneration levels may be linked to increasingly harsh microsite conditions, which become more relevant in filtering patterns of forest recovery (Kemp et al. 2019; Peven et al. 2024). Although we cannot state this conclusively, our findings suggest that future post-fire regeneration capacity could be diminished with increasingly hotter and drier conditions expected with climate change, as seed availability alone may not be sufficient to sustain *P. nigra* recovery after fire.

At the regional scale we observed distinct regeneration patterns, with seedling abundance varying among fires. Fires at the edge of *Pinus nigra's* range showed low regeneration rates, whereas those in the center of its distribution exhibited higher recovery rates. Although our study was conducted within only four fires footprints, this pattern concurs with the observed effects of precipitation. Accordingly, we interpret the negative relationship between precipitation and seedling abundance as a spatial artifact, as sites with higher precipitation in our dataset are located near the species' distributional edge. Catalonia as a region includes a pronounced elevation and precipitation gradient, from the lowlands to the Pyrenees, making it difficult to disentangle the effects of

climate from those of species distribution limits and the multivariable niche of black pine. In these peripheral areas, lower *P. nigra* regeneration may result from competition with other woody species (Rouget et al. 2001), which can colonize former *P. nigra* stands after fire. In our study, sites with higher precipitation showed greater abundance of resprouting angiosperm shrubs and trees (e.g. *Salvia rosmarinus*, *Quercus ilex*), which establish rapidly after fire and can outcompete smaller *P. nigra* seedlings (Rouget et al. 2001; Sánchez-Pinillos et al. 2018). After fires, these areas may transition to different forest or shrublands types regardless of *P. nigra* seed source availability, as suggested in previous studies in the region (Canelles et al. 2019; Enríquez-de-Salamanca 2023). However, further research is needed to disentangle climatic effects by explicitly controlling for the correlation between precipitation and distribution limits.

Environmental microsite drivers explaining the level of regeneration

Our results from the models of regeneration inside fire refugia suggest that canopy cover within refugia provides a sheltering effect on post-fire regeneration at high HLI levels, protecting it from the effects of the high radiation and aridity. Canopy cover can buffer the sharp climatic fluctuations found in open environments by regulating maximum and minimum temperatures, wind speed, radiation, and soil temperature (Balandier et al. 2022). This protective microclimate effect is especially important during summer droughts, as it can enhance the growth and survival of climate-sensitive juveniles (Meddens et al. 2018). Studies in dry forests of New Mexico, USA, have shown that fire refugia reduce maximum temperatures and increase relative humidity, improving regeneration success by mitigating harsh climate conditions (Marsh et al. 2022). Hence, fire refugia may help mitigate the effects of climate change on *P. nigra* populations compared to areas outside the canopy shelter (Zellweger et al. 2020; De Frenne et al. 2021).

However, the buffering effect of canopy may be counteracted by the reduced light availability within refugia. In our study, inside refugia, higher DWD levels inside refugia were associated with higher basal areas and higher stand densities, which can limit light availability and, therefore, regeneration success (Supplementary Table 4). Our results indicate that at higher DWD levels, regeneration abundance inside refugia is lower than outside refugia. This trend is only reversed at the lowest DWD levels (minimum DWD: 0 outside refugia and 1.03 inside refugia; Supplementary Fig. 3), where light availability inside refugia may no longer be a limiting factor, and regeneration outside refugia is primarily constrained by seed source distance (Martín-Alcón and Coll 2016). This decline in regeneration inside refugia with increasing DWD aligns with findings for ponderosa pine and Douglas-fir in the USA, where juvenile tree survival and growth were higher in areas with lower canopy cover (Hill et al. 2024). Similarly, studies of *P. nigra* in unburned sites report reduced survival and growth under high canopy cover (Gómez-Aparicio et al. 2006). Additionally, both greenhouse and field experiments suggest that moderate shade levels are optimal for *P. nigra* seedling recruitment and growth (Lucas-Borja et al. 2016; Tsakaldimi et al. 2021).

The light constraint inside refugia could also explain differences in regeneration levels inside and outside refugia across aridity gradients, if interpreted also as a metric of evapotranspiration demand or plant water limitation. We found that in low- to mid-aridity locations (HLI < 0.6), regeneration was more abundant outside refugia than inside. Conversely, in more arid sites, the sheltering microclimate effect of the canopy enhanced seedling establishment, suggesting that light availability was no longer the most limiting factor. Tíscar and Linares, (2013) found similar patterns in *P. nigra* populations across an aridity gradient in Spain, where canopy cover had a negative effect at the wettest sites but became beneficial as aridity increased. These findings align with broader research on the thermophilization of plant communities in Europe, which suggest that the buffering effect of forest cover mitigates the impacts of macroclimate in forests understories, and allows retaining species adapted to cooler conditions in the ecosystem (De Frenne et al. 2013).

Inside fire refugia, we observed that the understory community also limited the regeneration level of *P. nigra*, as shrubs competed with juvenile pines regardless of aridity levels. Similarly, De Lombaerde et al. (2019) also found that understory competition had a stronger influence on tree regeneration than adult tree abundance in Belgium. For *P. nigra,* higher survival rates have been reported in areas without shrub cover (Lucas-Borja et al. 2016). However, contrary

to our findings – where we found no combined effect between shrub cover and aridity inside fire refugia – simulation studies in Spain showed that seedling survival was higher under shrub cover in drier years, and lower during wetter years (Lucas Borja et al. 2021). Further research is needed to explore whether a similar interaction occurs inside fire refugia under post-fire conditions across a broader aridity gradient.

Outside refugia, heat load had a negative effect on post-fire regeneration, consistent with Gracia et al. (2002), who reported that *P. nigra* regeneration was limited to low-aridity areas. However, in our study, shrub cover mitigated this effect at sites with moderate to mid-low aridity. Similar results were observed for *Pinus pinaster* in France, where *Arbutus unedo* facilitated *P. pinaster* survival under intermediate water stress conditions (Guignabert et al. 2020). This sheltering effect of shrubs on seedling abundance could occur due to its shading effect, which creates a microclimate that buffers abiotic stress and reduces seedling mortality in xeric environments (Kunstler et al. 2006; Gómez-Aparicio et al. 2008). However, at high aridity levels, this facilitative effect in our study shifted to competition, likely due to neighboring plants depleting soil water resources and intensifying interspecific competition (Maestre et al. 2005). This shift aligns with Holmgren et al. (2012) who reported that facilitation can shift to competition at both ends of the aridity gradient (see also Maestre et al. 2009).

Gómez-Aparicio et al. (2004) found that the magnitude of facilitation depends on the interacting species; with some creating antagonism while others promote regeneration. In our study, *Rubus* spp. cover had a positive effect on *P. nigra* regeneration both inside and outside refugia, in contrast to the relationship we observed for total percentage of shrub cover. This positive effect could be partially related to facilitation, as spiny species (like *Rubus*) can reduce seed and plant predation (Olff et al. 1999; Alias et al. 2010). For instance, similar facilitative interactions – related to reduced seed predation – have been observed for *P. nigra* in unburned sites in Spain, in association with *Juniperus communis* (Tíscar 2003). However, part of this facilitative effect could also be explained by the reduction in evaporative demand for plants growing beneath this species, as we previously described for total shrub cover. Since *Rubus* spp. is also a nitrophilic species (Walter et al. 2016) its association with *P. nigra* could also be linked to microsite differences in soil nitrogen, a factor positively related with pine growth in various studies (Tsakaldimi et al. 2021; Barčić et al. 2022). Yet, preliminary results from soil analysis at our plots suggest that soil nitrogen content may not explain the positive interaction between *Rubus* spp. and *P. nigra* regeneration. Further research is needed to determine whether *Rubus* spp. enhances post-fire *P. nigra* regeneration through improved site conditions or via direct facilitation, such as protection from seed predation or seedling browsing.

Conclusion

Our study provides a broad understanding of the regeneration ecology of *P. nigra* in post-fire landscapes and demonstrates that beyond seed availability, biophysical microsite conditions play a key role in regeneration and set the stage for successional trajectories of black pine forests. Fire refugia modify local microsite conditions by reducing aridity, altering the effects of shrub cover and heat load index on regeneration compared to sites outside refugia. For sites outside of fire refugia where high severity has re-set successional cycles, shrubs provide a sheltering effect under mid-low aridity levels; however, as aridity increases, this effect diminishes and shifts toward competition. At the landscape scale, our findings indicate a decline in post-fire *P. nigra* recovery at the edge of its distribution, suggesting potential future shifts in forest composition. These areas may transition toward forests and shrublands dominated by resprouting species, with very different ecosystem composition, structure and function, highlighting the need for further research on the long-term resilience of *P. nigra* in fire-prone landscapes and ecosystem transitions in the context of global change.

Acknowledgements The Ministry of Science and Innovation of Spain funded this research through the projects UMBRACLIM (PID2019-111781RB-100), VULNIFOR (PID2022-142108OB-I00), and the predoctoral grant PRE2020-094807. Ana Lucia Mendez-Cartin benefited from the Marie Skodowska-Curie Research and Innovation Staff Exchange (RISE)—grant agreement Nr: 101007950. Aitor Ameztegui is supported by a Serra-Húnter fellowship. The authors are grateful to Gil Torné for his support in fieldwork and to the personnel of the Sant Llorenç del Munt National Park for all their help during our fieldwork. We are also grateful to everyone in the USFS in Corvallis, who helped achieve

Ana Lucia's internship—crucial to this paper—with special thanks to David Bell, who hosted and assisted Ana Lucia while she was in Corvallis. We also like to thank Dustin Gannon for all his aid in statistics.

Author contributions All authors contributed to the study conception and design. Material preparation and data collection was performed by Ana Lucia Mendez-Cartin, Pere J. Gelabert and Anna Fontova. The analysis was done by Ana Lucia Mendez-Cartin, Aitor Ameztegui, Lluis Coll and Meg Krawchuk. The first draft of the manuscript was written by Ana Lucia Mendez-Cartin and all authors commented on previous versions of the manuscript. All authors read and approved of the final manuscript.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This worked was supported by the Ministry of Science and Innovation of Spain through the project UMBRACLIM (PID2019-111781RB-100), VULNIFOR (PID2022-142108OB-I00), and the predoctoral grant PRE2020-094807. Ana Lucia Mendez-Cartin benefited from the Marie Skodowska-Curie Research and Innovation Staff Exchange (RISE)—grant agreement Nr: 101007950. Aitor Ameztegui is supported by a Serra-Húnter fellowship.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest All authors declare that neither one has any financial interest nor personal relationships that could have influenced inappropriately the work of this paper.

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