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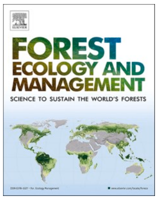

Canopy cover and species' climatic niche shape *Pinus sylvestris* regeneration after drought-induced die-off

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ABSTRACT

Drought-induced die-off alters canopy structure and understory microclimatic conditions, but its consequences for tree regeneration remain unclear. We assessed how canopy-driven microclimate filtering and climatic suitability influenced *Pinus sylvestris* regeneration across developmental stages (seedlings, young saplings, and old saplings) following drought-induced die-off in forests across Catalonia (NE Spain). We analysed recruit densities with linear mixed models incorporating forest condition (die-off vs. control), canopy type (closed, defoliated, and open gaps), survey year (2013, 2017, and 2022), and climatic-niche metrics as fixed effects, while site and plot were considered as random effects. In closed habitats, die-off lowered both young and old saplings relative to controls. Defoliated habitats consistently failed to support regeneration across all stages, even in climatically favourable sites, likely due to impaired propagule supply. Open habitat enhanced seedling and sapling densities in die-off plots. Regarding the position in the climatic niche, old saplings persisted in closed habitats at climatically marginal sites, likely benefiting from canopy-mediated microclimate control. Canopy buffering also protected young saplings in closed habitats during the periods with strong interannual climate fluctuations. In open habitats, young and old saplings were sensitive to climatic position in species' niche, with their densities declining with increasing distance to the optimum, core niche. Overall, seedlings' density was higher near the climatic optimum in die-off plots than in controls. Also, nearly a decade after the drought, only young sapling densities increased in die-off plots, likely reflecting disturbance legacies and favourable climatic fluctuations. Our results highlight the silvicultural value of maintaining a mosaic of canopy structures, retaining open habitats in climatically optimal sites to enhance seedling establishment and progression, while preserving closed canopy refugia in marginal climatic sites to buffer climate extremes, thus, favouring saplings survival against increasing drought stress.

1. Introduction

Ongoing climate change is increasing the frequency and severity of droughts, triggering widespread tree mortality and forest die-off across various forest types and biomes (Allen et al., 2015; Anderegg et al., 2015). This phenomenon poses significant challenges to forest regeneration and potentially alter the forest succession process (Anderson et al., 2025; Xu et al., 2024). Water-limited Mediterranean forests are particularly vulnerable to large-scale drought-induced tree die-off, leading to shifts in dominant species, which might eventually initiate ecosystem collapse (Dorado-Liñán et al., 2019; Galiano et al., 2013; Lloret and Batllori, 2021). As a result, forests may experience an immediate and significant decline in biodiversity, ecosystem functions and services, thereby disrupting soil-atmosphere interactions (Anderegg et al., 2013). Paradoxically, such disturbances may also create opportunities for an ecological reset in the affected forest stands. Specifically, the opening of gaps and the accumulation and decay of deadwood promote forest heterogeneity, that, concomitant with reduced

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competition, may enhance stand biodiversity by allowing different species to establish and modify the community composition (Batllori et al., 2020; Chowdhury et al., 2024, 2025). This dual nature of drought-induced die-offs, involving both destructive and regenerative processes (i.e., disturbance paradox; see Thom and Seidl, 2016) can lead to less predictable successional trajectories. Yet, the long-term effects of drought-induced forest die-off on plant community dynamics remain difficult to anticipate due to the complexity of the different processes involving forest ecosystems functioning under climate change (Lloret and Batllori, 2021; Martínez-Vilalta and Lloret, 2016).

Successional trajectories after die-off are shaped, in addition to adult performance, by both the regeneration success and the pre-disturbance composition of advanced regeneration stages belonging to dominant and co-dominant canopy tree species (Gazol et al., 2018). Canopy mortality often triggers competition release by increasing light, water, and nutrients availability, which in turn promotes the rapid growth of previously suppressed saplings (Chowdhury et al., 2025). Two short-term main successional pathways can be recognized afterwards: self-replacement (i.e., auto-succession), in which the dominant, affected species re-establishes and replacement, where a co-dominant or different species reaches dominance (Lloret and Batllori, 2021; Margalef-Marrase et al., 2022). In Mediterranean-type forests, the resulting successional pathways tend to favour shade-tolerant species with drought-adaptive traits, such as efficient water-use strategies (Lloret et al., 2012; Martínez-Vilalta and Lloret, 2016), in addition to those with the ability to resprout (Zeppel et al., 2015). Ultimately, the ability of dominant species to recover following drought-induced die-off may be outcompeted by more resilient co-dominant species, whose functional traits and regenerative strategies confer them a competitive advantage in the successional process (Lloret and Batllori, 2021; Martínez-Vilalta and Lloret, 2016). Also, other species may migrate from surrounding areas through seed or propagule dispersal (Selwyn et al., 2024), although competition, facilitation, and priority effects (i.e., the order in which species arrive) will determine which species ultimately establish successfully (Fukami, 2015; Maestre et al., 2009).

Climate conditions also shape regeneration based on the species-specific climatic niche requirements (Grubb, 1977; Pironon et al., 2018). The species' climatic niche can be quantified by constructing bioclimatic hypervolumes that capture the range of environmental conditions associated with known occurrences of the species. However, ongoing shifts in temperature and precipitation induced by climate change may narrow the extent of the historic suitable climatic ranges, pushing many species toward the limits of their climatic tolerance (Rehm et al., 2015). This pattern is described within the "core vs. edge" framework, i.e., species would tend to perform better at the core of their climatic niche, where environmental conditions align with their physiological and evolutionary optimum (Perez-Navarro et al., 2019; Pironon et al., 2018). Yet, populations in these locations may also suffer high mortality during drought episodes likely due to their acclimatation to mild, favourable conditions (Elvira et al., 2021; Lloret and Kitzberger, 2018). In turn, populations placed close to the edges of their climatic niches are expected to perform worse and may be particularly vulnerable during drought episodes (Perez-Navarro et al., 2021, 2019). Otherwise, these edge populations may also be adapted to local conditions such as extreme weather, thereby experiencing reduced mortality during drought events (Margalef-Marrase et al., 2022). Also, tree regeneration is expected to decline after drought due to climatic stress, given that recruits (seedlings and saplings) typically have more restrictive niche requirements than adults (Elvira et al., 2021; Grubb, 1977; Jackson et al., 2009). Yet, regeneration success may recover once climate conditions become favourable again, provided that sufficient regenerative material remains in the system (Grubb, 1977; Jackson et al., 2009). Interestingly, regeneration even could be maintained if the climatic buffering provided by the canopy of surviving trees is sufficient to support and promote seedling establishment. This facilitative process, named as canopy service, may help and sustain the regeneration event in populations located away from the species' climatic optimum (Margalef-Marrase et al., 2025). As a result, canopy cover can contribute to a mismatch between species climatic requirements and its actual distribution (Perez-Navarro et al., 2024).

Local climatic conditions are strongly influenced by canopy cover (De Frenne et al., 2019). Following drought-induced die-off, the degree of sunlight penetration governs microclimatic conditions beneath the canopy by influencing temperature and soil moisture conditions (Thom et al., 2020). In those situations, canopies of surviving trees can buffer climatic extremes and create localized refugia that support recruit's establishment (Perez-Navarro et al., 2024; Thom et al., 2023), particularly for shade-tolerant species. This canopy-driven facilitation may prolong the persistence of the regeneration of dominant species in the forest stand by extending local extinction lags under ongoing adverse microclimatic conditions (Alexander et al., 2018). Additionally, tree mortality increases deadwood accumulation, potentially contributing to favourable habitats for seedling establishment by providing shade, retaining moisture, and protecting them against desiccation and predation (Hagge et al., 2019). However, stands with extensive canopy loss could experience reduced structural buffering compared to the dense canopy cover, resulting in higher temperatures and lower relative humidity at the forest floor. These harsher conditions can hinder seedling establishment and survival (Schmidt et al., 2017; Thom et al., 2020), potentially leading to regeneration bottlenecks (Gazol et al., 2018). Under these conditions, the trajectory of forest regeneration is likely to be shaped by the adaptive capacity of accompanying tree species, particularly those able to tolerate projected climatic extremes.

Pinus sylvestris L. (Scots pine) is a long-lived, shade-intolerant conifer with wind-dispersed seeds and is one of the most widely distributed conifer species across the Northern Hemisphere, especially in Europe (Fig. 1A, Bose et al., 2024). While it has traditionally been considered as a relatively drought-tolerant species, it has shown increasing vulnerability to climate-induced die-off across its distribution range, including core and marginal climatic zones of temperate and Mediterranean regions (Bose et al., 2024; Margalef-Marrase et al., 2023). Although mortality and die-off events in *P. sylvestris* forests reduce stand biomass, they also contribute to higher structural complexity over time through deadwood accumulation and changes in woody plant composition (Chowdhury et al., 2024, 2025). These changes may alter microclimatic conditions in habitats with variable canopy cover, from open sites to defoliated canopies and intact, closed canopies (Margalef-Marrase et al., 2022). Because *P. sylvestris* has high light requirements for seedling establishment and survival (Carlisle and Brown, 1968), its regeneration success is likely dependent on canopy openness. However, it is still poorly understood how the interaction of canopy openness and drought can affect the success of *P. sylvestris* regeneration following die-off events, and how this response varies depending on the population's position within the species' climatic niche. To address this knowledge gap, we have analyzed the density of recruits at different development stages in a paired plot design, including plots affected by drought-induced die-off and unaffected ones across Catalonia (NE Spain), a region covering a wide range of climatic conditions. Specifically, we hypothesize:

i) *P. sylvestris* recruit density will be higher in die-off plots due to reduced competition following overstory mortality and favourable light conditions for this species.
ii) *P. sylvestris* recruit density will vary under different canopy conditions, likely reflecting differences in regeneration success driven by varying microclimatic buffering provided by canopy cover.
iii) Recruit density will decline with increasing distance from the species climatic niche optimum (i.e., centroid), consistent with the core vs. edge framework. However, this trend may be modulated by different canopy conditions.

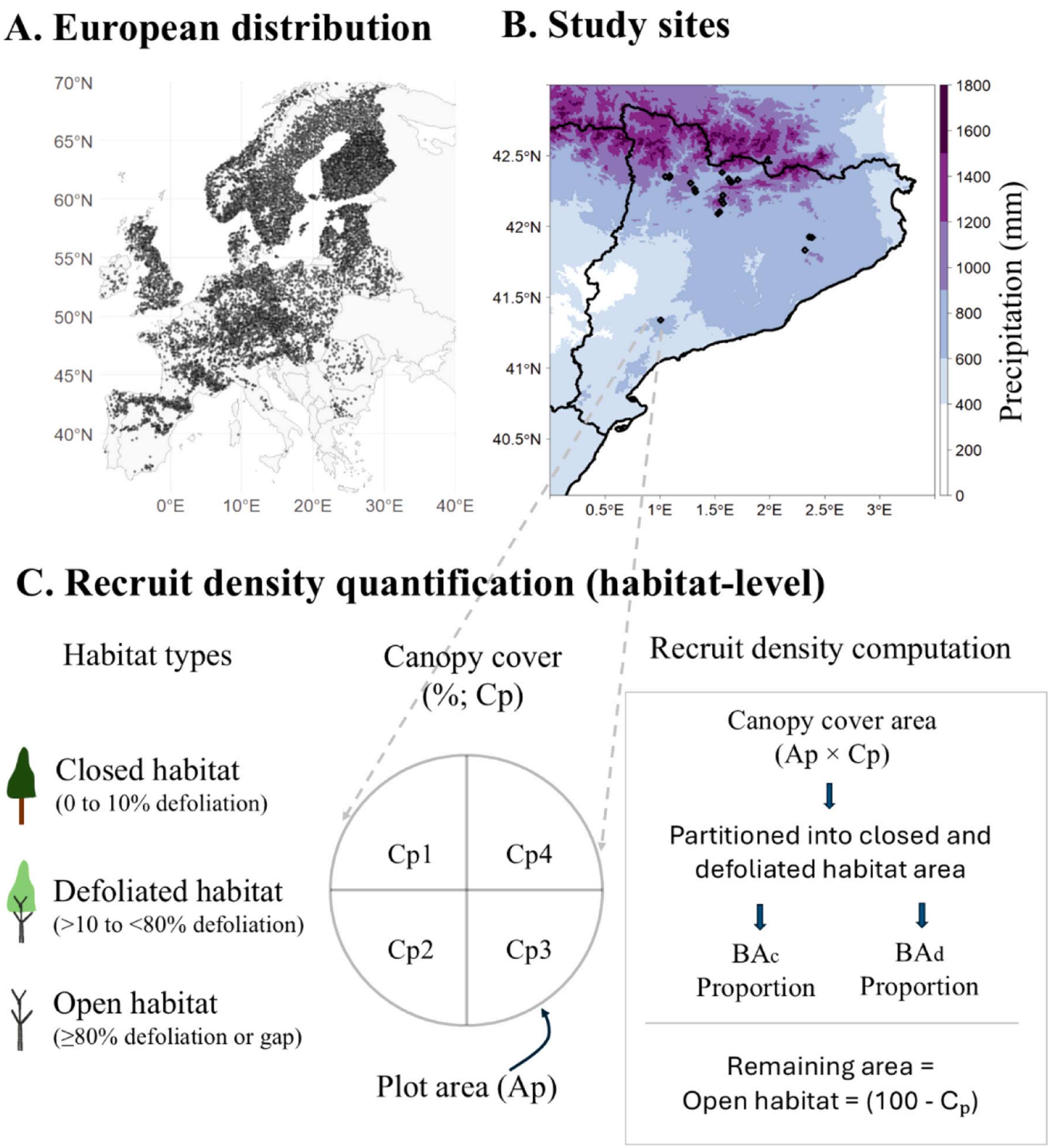

Fig. 1. (A) European distribution of *P. sylvestris*, (B) Study sites across Catalonia (NE Spain) shown over a precipitaion gradient (data source: Fick and Hijmans, 2017), and (C) Schematic representation of habitat-level recruit density *quantification*. Left: three canopy-cover habitats were distinguished based on defoliation of overstorey trees: closed habitat (0-10 % defoliation), defoliated habitat (>10-<80 % defoliation), and open habitat (≥80 % defoliation including dead tree or gaps). Middle: plot canopy cover (C_p) was visually estimated from four quadrants within each circular plot ($A_p = 314$ m^2). Right: the canopy-covered area ($A_p \times C_p$) was then partitioned into closed and defoliated habitat areas according to the basal area proportion of trees in each defoliation class (BA_c and BA_d). The remaining area (100 - C_p) was considered open habitat. Recruit density in each habitat type was calculated using Eqs. 1–3 in the Methods.

2. Methods

2.1. Study area

We studied forests dominated by *P. sylvestris* in Catalonia (NE Spain), as they have experienced drought-induced die-off and tree mortality in recent decades (Margalef-Marrase et al., 2023). These impacts were particularly severe following the 2012 drought, which was further exacerbated by bark beetle infestations (Jaime et al., 2019). *P. sylvestris* reaches its southernmost and driest distribution limit in the Iberian Peninsula, allowing to investigate its regeneration under bioclimatic limiting conditions. Accordingly, we surveyed twenty forest sites (Fig. 1B, Table S1), with a mean distance of 52.4 km among them (range: 14.7–90.1 km) covering a wide elevation (range: 600–1650 m a.s.l.) and climate gradients (ranging from cold-wet conditions in the Pyrenees to drier-warmer conditions in the Catalan Coastal Range; Figure S1, Table S1). Mean annual temperature was 10.3°C (ranging from 6.5 to 13.9°C), and annual precipitation was 774 mm (ranging from 341 to 1427 mm). During the drought-affected year (2012), mean annual precipitation dropped to 580 mm (ranging from 467 to 667 mm), while mean temperature remained similar (10.5°C; ranging from 8 to 13.3°C) across the studied area, indicating a severe precipitation deficit relative to the long-term mean. The composition of the sites, which was once dominated by pure *P. sylvestris* and mixed stands with *Quercus ilex* and *Q. humilis*, is transitioning into a more drought-tolerant and diverse Mediterranean woodland with an increasing presence in the canopy and the regeneration layer of *Quercus*, *Acer*, *Crataegus*, and *Prunus* species (Chowdhury et al., 2025).

2.2. Sampling design and data collection

In 2013, two circular-paired plots with a 10-meter radius (314 m^2) were established in each of the twenty forest sites (Fig. 1B, Table S1). One plot was located in a stand showing clear signs of drought-induced tree die-off and mortality, characterized by recently dead trees due to the 2012 drought (die-off plot), while the second plot was positioned 50–150 m away in a visually unaffected stand (control plot; see plot characteristics in Chowdhury et al., 2024; Margalef-Marrase et al., 2023). This paired plot design allowed direct comparisons between affected and unaffected forest conditions, while minimizing variability in environmental, topographical, and soil properties. No salvage logging occurred at the affected sites following the die-off, enabling the observation of *P. sylvestris* forest succession in natural conditions.

All *P. sylvestris* recruits ($\leq$ 2.5 cm DBH, diameter at breast height) were identified and counted at the plot level in 2013 and categorized into three developmental stages: T1, corresponding to seedlings under two years old with height $\leq$ 30 cm; T2, corresponding to young saplings older than two years with height $>$ 30 cm but $<$ 130 cm; and T3, corresponding to old saplings with height $\geq$ 130 cm but with DBH $\leq$ 2.5 cm (LIFE RedBosques, 2019). Resampling was conducted in all plots in 2017 and 2022 following the same procedure. Additionally, in each survey, we also visually identified the habitat where recruits grew, based on the overstorey over them. More precise methods to quantify canopy cover, for instance by hemispherical photography were discarded for operational purposes given that the presence of large number of recruits. Specifically, we recognized three canopy cover types based on the tree defoliation classes (Michel et al., 2023): (i) closed habitat, which consisted of canopies of alive trees with 0–10 % defoliation; (ii) defoliated habitat, which consisted of canopies of alive trees with more than 10 % but less than 80 % defoliation; and (iii) open habitat or gaps, which consisted of alive trees with 80 % or more defoliation, standing dead trees or open spaces with no trees (Fig. 1 C; Figure S2, S3).

We also measured the DBH of all alive trees with a DBH $>$ 2.5 cm in 2013, 2017, and 2022 to estimate tree basal area in each canopy cover type (Figure S2). While measuring DBH, we also visually estimated the defoliation level of each tree to allocate them to the above-mentioned canopy cover types (Fig. 1 C, Figure S3). Tree defoliation was characterized as the loss of leaves in relation to pre-established healthy trees, ranging from 0 % (fully green or closed canopy) to 100 % (fully defoliated or dead tree). This procedure is widely employed in studies characterizing forest die-off (Gazol et al., 2018; Sapes et al., 2017) and is supported by photographical records of given levels of defoliation for visual comparison. The reliability of the procedure was further underpinned by cross validation between different surveyors. During the 2017 and 2022 surveys, newly incorporated trees that had reached a DBH $>$ 2.5 cm were identified by comparing data from previous surveys and we measured their DBH and defoliation level.

2.3. Quantification of recruit density

The estimation of recruit density in each habitat category required an estimation of the area of each canopy cover type, which was unsuitable to be directly obtained in the field due to the canopy overlapping of trees with different level of defoliation (Figure S3). Therefore, we used to approximate the area corresponding to each canopy cover type through a proxy based on the basal area and the defoliation level of alive trees, combined with the overall plot canopy cover (Fig. 1C, Figure S3). First, in 2022, each plot was divided into four quadrants - to reduce errors relative to a single measurement -, where the percentage of canopy cover (0–100 %) was visually estimated. The mean plot canopy cover of the four quadrants was used to estimate the overall canopy cover (%) of the plot (C_p; Figure S3). Next, we calculated the approximate canopy-covered area of each plot by multiplying C_p with the actual plot area ($A_p = 314$ m^2). Then we split the canopy-covered area of each plot into the two habitat categories -closed and defoliated-, considering the proportion of the plot basal area of trees belonging to each canopy cover category. Specifically, the basal area of the closed habitat (BA_c) was calculated by summing the basal area of tree individuals with 0–10 % defoliation, while the basal area of defoliated habitat (BA_d) was calculated by summing the basal area of individuals with more than 10 % but less than 80 % defoliation. Then, the proportion of closed canopy habitat was defined as the ratio of BA_c to total alive tree basal area ($BA_c + BA_d$), and this value was multiplied by the overall canopy area in the plot ($C_p \times A_p$) to estimate the area of closed habitat. Similarly, the area of the defoliated habitat was calculated as the ratio between BA_d and total alive tree basal area under canopy cover ($BA_c + BA_d$), which was then multiplied by the canopy area ($C_p \times A_p$). Finally, the area of the open habitat (C_o) was calculated as the proportion of open gaps (i.e., 100 minus canopy cover of plot, 100 - C_p) and multiplied by plot area (A_p). We did not include the basal area of alive trees with 80 % defoliation or more when estimating the area of the open canopy cover, as recruits under these trees received no partial canopy shedding like in the open spaces with no trees.

These habitat-specific areas were used to calculate recruit densities in each habitat by dividing the number of recruits observed in closed (N_c), defoliated (N_d) and open (N_o) habitat by the respective habitat area (Eqs. 1, 2 and 3).

$$\text{Recruits' density in closed habitat } \left(\text{no.}\middle/\text{ha}\right), \quad D_c = \frac{N_c \times 10000}{\left(\frac{A_p \times C_p}{100}\right) \times \left(\frac{BA_c}{BA_c + BA_d}\right)} \tag{1}$$

$$\text{Recruits' density in defoliated habitat } \left(\text{no.}\middle/\text{ha}\right), \quad D_d = \frac{N_d \times 10000}{\left(\frac{A_p \times C_p}{100}\right) \times \left(\frac{BA_d}{BA_c + BA_d}\right)} \tag{2}$$

$$\text{Recruits' density in open habitat } \left(\text{no.}\middle/\text{ha}\right), \quad D_o = \frac{N_o \times 10000}{A_P \times \left(\frac{(100 - C_P)}{100}\right)} \tag{3}$$

Where, 10,000 converts the result from recruits per m^2 to recruits per hectare (ha), and the denominator of 100 converts canopy cover from percentage to proportion.

2.4. Quantifying the historical climate niche and plot niche matrices of *P. sylvestris*

We obtained 9351 unique occurrence records of *P. sylvestris* populations from the EU-Forest dataset (i.e., European tree species distribution) to construct the species historical climate niche (Mauri et al., 2017). For each of these locations, we extracted daily minimum temperature, daily maximum temperature, and daily precipitation by means of the *easyclimate* R package for 1980–2021 period (Cruz-Alonso et al., 2023).

From these daily data, we calculated monthly values to derive yearly bioclimatic variables, allowing us to characterize the interannual variability in the environmental conditions experienced by the species (Perez-Navarro et al., 2021). Specifically, we computed 19 standard yearly bioclimatic variables (i.e., BIO1 to BIO19; see Table S2) over the 42-year period using the R package *dismo* (Hijmans et al., 2024). Among the bioclimatic variables, 12 were used to construct an environmental climatic space through a principal component analysis (PCA) using the *ade4* R package (Dray and Dufour, 2007; Table S2), according to Perez-Navarro et al. (2021). The first principal component (PC1 / Dim1) accounted for 41.2 % of the total variance, while the second principal component (PC2 / Dim2) explained an additional 32.1 %, indicating an overall good fit of the PCA (Fig. 2A). Variables like bio12, bio13, bio14, bio16, and bio17 (related to precipitation) showed a strong positive relationship with Dim1 and a moderate positive correlation with Dim2 (Fig. 2 A). Meanwhile, bio1, bio6, bio10, and bio11 (temperature-related) showed a negative relationship with Dim1 and Dim2 (Fig. 2A). Furthermore, bio4 (temperature seasonality) showed a negative relationship with Dim1 but a positive one with Dim2 (Fig. 2A).

Subsequently, we applied kernel density estimation with *ks* R package (Chacón and Duong, 2018) to determine the density of *P. sylvestris* European occurrences within a two-dimensional environmental space. From this, we identified the *P. sylvestris* climatic niche using the 5–95 % kernel density contours, representing the realized climatic niche of the species (Fig. 2B). Within this climatic niche, we characterized the core (i.e., niche centroid) corresponding to the area of highest occurrence density in the climatic space, and the boundaries (i.e., niche edge) which reflects the species' tolerance limits (Fig. 2B). Next, we determined the relative positions within the realized climatic niche of our study plots during the 2000–2021 period (Figure S4), accounting for the estimated period of recruitment occurrences (Table S3) and using 2021 as the last year to capture a full annual cycle, since the third survey was conducted in summer 2022. To do that, we translated the values of the 12 annual bioclimatic variables for that period (Table S2) to the above-mentioned environmental climatic space (i.e., the PCA; Fig. 2 A) by using the *sub-row* function of *ade4* R package (Dray and Dufour, 2007). To characterize the position of each plot within the species' climatic niche in every year during 2000–2021, we calculated the Euclidean distance between each position and the niche centroid (core distance, hereafter; Fig. 2B, Figure S4). We used this methodology instead of percentiles or other climate suitability metrics given that some locations of the study plots moved beyond the limits of the niche in several years of the period assessed (Perez-Navarro et al., 2021).

We used different periods to account time windows relevant to each recruit stage: four years prior to sampling for T1, eight years prior to sampling for T2, and twelve years prior to sampling for T3 stage (Table S3). For each sampled year and developmental stage, we computed the sites' mean Euclidean distances to calculate distances to core for each time window for each survey. To capture temporal climatic variability, we also calculated the coefficient of variation (hereafter, core distance CV) of these distances for each stage across the three sampled years.

2.5. *Statistical analyses*

To investigate the combined effects of the die-off event (reflecting die-off and control plots) across time (2013, 2017, and 2022), canopy types (closed, defoliated, and open), and niche metrics, i.e., position in the species climatic niche, we constructed separate linear mixed models (LMMs) with recruits' density at each developmental stage (T1, T2, and T3) as the response variable. In these models, fixed effects were forest condition (die-off and control), survey year, canopy types, and niche metrics (core distance and core distance CV). Interaction terms up to the second order were incorporated in the full model. Both site and plot identity were treated as random effects to account for the paired plot design and repeated measures across survey years, respectively.

To further assess the impact of forest die-off on the recruitment in the specific survey year we constructed individual LMMs for each developmental stage at each survey year using recruits' density as the response variable. In these models, forest condition was included as fixed effect and site identity was incorporated as a random effect to account for the paired design of our sampling. Besides die-off, we also developed individual LMMs to evaluate the influence of canopy cover variations on the recruitment at each specific survey year. Recruits' density at each developmental stage was used as the response variable and canopy types was the fixed effect. Site and plot identity were included as random effects to account for the paired plot design and repeated measures across survey years, respectively. Finally, to assess the effect of forest condition within each canopy type and development stage, we performed separate Tukey HSD tests comparing die-off and control plots, for each canopy type and development stage by pooling data without considering the survey years.

The LMMs were implemented using the *lmer* function from the *lme4* R package (Bates et al., 2024; R Core Team, 2024). Continuous

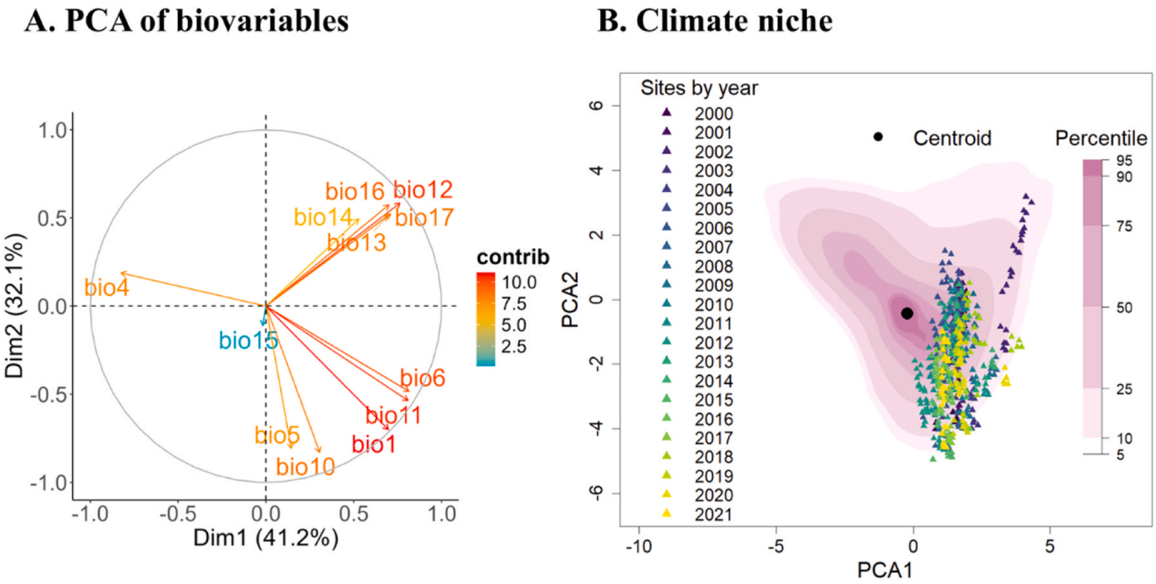

Fig. 2. (A) Biplot of principal component analysis (PCA) with 12 bioclimatic variables indicating their relative contributions to the first two principal components (Dim1 and Dim2), and (B) climate niche of *P. sylvestris* in the PCA *space* (at 5–95 % kernel density contours), indicating the centroid (black dot), and showing the study site positions by year (2000–2021). Year-specific site distributions are detailed in Fig. S4.

explanatory variables were scaled, and model selection was performed using the *dredge* function for fixed and random factors using the *MuMIn* package, based on AIC with a threshold of 2 (Barton, 2024).

3. Results

Seedling-stage (T1) density of *P. sylvestris* did not differ significantly between forest condition, either when data were pooled across years (Table 1, Table S4) or when assessed separately for 2013, 2017, and 2022 (Table S5). Moreover, no differences were observed between canopy habitats when data were pooled across the studied period (Table 1, Table S4). However, across survey years, open habitats consistently supported higher T1 densities than defoliated ones (Table 2; Table S6). In 2013, T1 recruitment was also higher in closed habitats than in defoliated ones (Table 2; Table S6). T1 recruits were more abundant in die-off plots under open canopy (Fig. 3A, Figure S5A), as reflected in the interaction between open canopy and die-off (Table 1, Table S4), but pair comparisons between die-off and control plots for T1 recruits in open canopy failed to obtain statistical significance (Figure S5A). Regarding niche determinants, the density of T1 recruits in die-off plots declined with increasing distance to the core (Fig. 4; Table 1).

Young sapling recruits (T2) also showed no significant differences between forest condition when data were pooled without considering distinct years (Table 1, Table S7) or the three survey years individually (Table S8). Regarding canopy type, closed habitats exhibited significantly higher T2 densities than defoliated ones when data were pooled across the surveys (Table 1, Table S7). Meanwhile, T2 density was significantly higher in open habitats compared to defoliated habitats in each survey year (Table 2, Table S9). Also, in 2013, T2 density was higher in closed habitats compared to defoliated ones (Table 2, Table S9). Open habitats in die-off plots (136 ± 32 saplings/ha) exhibited higher T2 density compared to control ones (44 ± 15 saplings/ha), whereas closed habitats in die-off plots (22 ± 8 saplings/ha) showed a lower density relative to control ones (112 ± 38 saplings/ha; Figure S5B), as reflected by the significant interactions between canopy habitats and forest condition (Table 1; Table S7; Fig. 3B). Besides, T2 density increased in die-off plots by 2022, whereas T2 recruitment in control plots remained relatively stable across years (Fig. 5A; Table 1). Climatic niche metrics determined T2 recruitment by their interactions with canopy habitat (Fig. 6A, B; Table 1). T2 density declined with increasing core distance in both closed and open canopy habitats, whereas in defoliated habitats recruitment was not affected by increasing core distances in the climatic niche (Fig. 6A; Table 1). Besides, T2 recruitment was higher in closed habitat when core distance CV was high (Fig. 6B; Table 1).

Table 1

Estimates from linear mixed models (LMMs) assessing the effects of drought-induced die-off (compared to control), canopy cover types (closed, defoliated, open), and niche metrics (core distance and core distance coefficient of variance, CV) on *P. sylvestris* recruits at different development stages (T1, T2, and T3; see Methods) across three survey years (2013, 2017, and 2022) in forests from Catalonia (NE Spain). Marginal and conditional R^2 values are also given. Detailed model specifications and additional results are provided in the Supplementary Materials.

	Estimates		
Predictors	T1 stage	T2 stage	T3 stage
Die-off	-0.33	-66.71	-13.59
Closed habitat	17.74	156.03***	52.58***
Open habitat	18.89	70.06	6.77
2017		-6.47	0.13
2022		0.92	-3.97
Core distance	2.91	-0.01	-1.82
Core distance CV	-1.99	18.49	
Die-off: Closed habitat	-4.43	-75.26*	-24.49*
Die-off: Open habitat	39.04*	107.75**	38.20***
Die-off: 2017		56.18	8.10
Die-off: 2022		105.47**	19.38
Closed habitat: 2017		-63.00	-27.43
Open habitat: 2017		-49.11	-6.18
Closed habitat: 2022		-117.54	-37.32**
Open habitat: 2022		-79.62	4.30
Die-off: Core distance	-18.30*		
Closed habitat: Core distance		-50.92*	-9.63
Open habitat: Core distance		-84.66***	-17.13**
Closed habitat: Core distance CV	-3.19	-23.42	
Open habitat: Core distance CV	-16.47	-68.80*	
Marginal R^2 / Conditional R^2	*0.10 / 0.15*	*0.18 / 0.41*	*0.18 / 0.33*

[*] $p < 0.05$
[**] $p < 0.01$
[***] $p < 0.001$

Table 2

Estimates from linear mixed models (LMMs) assessing the effect of canopy cover types (closed, defoliated, open) on *P. sylvestris* recruits at different development stages (T1, T2, and T3; see Methods) across three survey years (2013, 2017, and 2022) in forests from Catalonia (NE Spain). Marginal and conditional R^2 values are also given. Detailed model specifications and additional results are provided in the Supplementary Materials.

		Estimate		
Development stage	Canopy cover type	2013	2017	2022
T1	Closed	35.38*	1.99	9.20
	Open	32.47*	17.50*	65.25**
T2	Closed	108.26**	56.99	9.39
	Open	81.25*	79.55*	82.27**
T3	Closed	40.17**	14.26	1.83
	Open	25.58*	22.09*	28.05*
	Marginal R^2 / Conditional R^2	0.06 / 0.11	0.04 / 0.04	0.08 / 0.08

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Recruitment at the old sapling stage (T3) showed no significant differences between forest condition, whether analysed using pooled data (Table 1, Table S10) or separately for 2013, 2017, and 2022 (Table S11). Regarding canopy habitat, only closed canopy habitats had higher older saplings compared to defoliated ones when data were pooled across surveys (Table 1, Table S11). However, open habitats consistently supported significantly higher T3 recruitment compared to the defoliated ones in 2013, 2017, and 2022 (Table 2, Table S12). Also, closed habitats exhibited higher T3 recruitment than defoliated ones in 2013 (Table 2, Table S12). Open habitat in die-off plots showed higher T3 density (45 ± 12 saplings/ha) than in control ones (12 ± 4 saplings/ha), while closed habitat in die-off plots (8 ± 2 saplings/ha) had lower density compared to control ones (37 ± 8 saplings/ha; Figure S5C), as reflected by the interactions between canopy habitats and forest condition (Fig. 3C; Table 1). Regarding temporal changes, T3 recruitment in closed habitats declined by 2022 (Fig. 5B; Table 1). Finally, core distance was negatively associated with T3 density in open habitats compared to defoliated ones (Fig. 6C; Table 1).

In general, the linear mixed models explained only a small part of the variability of the data when forest condition and canopy cover type were included as a single fixed factor, also considering the random effects in the model (Table S5, S6, S8, S9, S11, S12). However, despite low marginal R^2 values in models with multiple fixed factors, the conditional R^2 increased when the random factors (site and plot) were included.

4. Discussion

Drought-driven defoliated habitats consistently failed to support regeneration across all recruits' developmental stages throughout the nine-years study period, and this limitation persisted even at sites that were considered climatically suitable for *P. sylvestris*. The position of

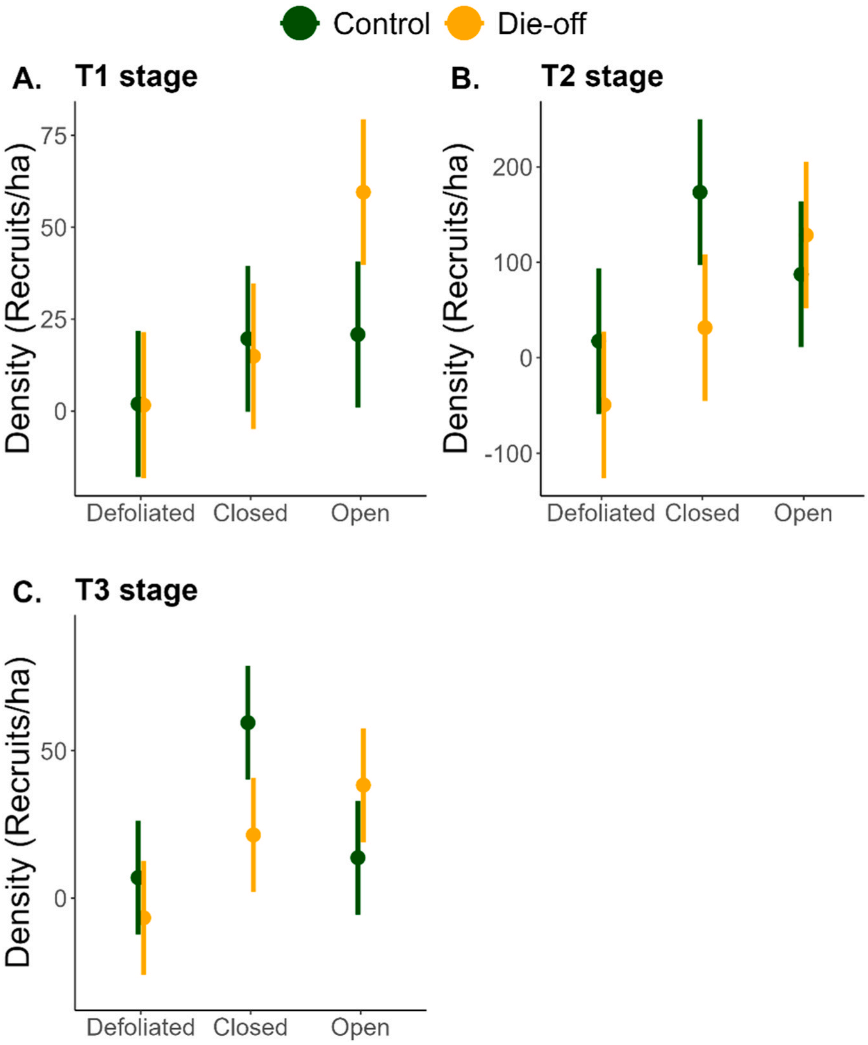

Fig. 3. *Pinus sylvestris* density (recruits/ha) for the studied development stages (A) T1 (seedlings), (B) T2 (young saplings), and (C) T3 (old saplings) in the different canopy cover types (closed, defoliated, and open), based on data pooled across years. The figure reflects model predictions. The dots denote point estimates, while error bars represent 95 % confidence intervals. Model summary and statistical significance of the interaction effects are provided in Table 1.

populations in the species climatic niche explains regeneration in open habitat, particularly in young and old saplings stages, as their density declined at sites located farther from the core of the species' climatic niche. Interestingly, old saplings persisted in marginal sites under closed canopies, pointing to the potential buffering role of canopy cover (Perez-Navarro et al., 2024).

4.1. Canopy cover type effect on regeneration success

The effect of die-off in *P. sylvestris* recruitment was strongly associated to its interaction with the microlocal modification of canopy-cover. The reduced recruitment in defoliated habitats was likely due to severely defoliated *P. sylvestris* trees that, although survived the drought, they experienced severe damage, and probably produced few viable cones or poor-quality seeds, limiting propagule availability (Galiano et al., 2013; Vilà-Cabrera et al., 2015).

In contrast, open habitat in die-off plots favoured the establishment of new seedlings and its successive development stages (i.e., young and old saplings; Fig. 3), likely due to increased light availability associated with reduced competition. *P. sylvestris* reproduction is highly influenced by light availability, as cone opening and seed germination typically require favourable irradiance and thermal conditions (Carlisle and Brown, 1968). Therefore, competition release following die-off allowed light-demanding *P. sylvestris* seedlings to establish successfully and progress toward next developmental stages.

In turn, young and old saplings were more abundant in the closed habitats than in the defoliated ones (Table 1), particularly in control plots (Figs. 3B, 3C, Figure S5B, S5C), where canopy cover was maintained (Figure S3). This likely strengthened canopy cover-mediated microclimatic buffering by reducing temperature extremes and maintaining higher soil moisture, which in turn favoured the survival of young saplings and their progression into old stage (Keppel et al., 2017). However, sapling densities declined in the closed habitats of die-off plots (Figure S5B, S5C), suggesting that drought not only triggered the mortality of overstory adult *P. sylvestris* trees in these plots but also reduced the survival of understory saplings. In closed habitats of die-off plots, recruits also faced competition from both surviving *P. sylvestris* individuals and co-occurring drought-tolerant species. This competition likely limited the self-replacement potential of *P. sylvestris*. In turn, advanced regeneration belonging to more drought-resilient species (e.g. *Quercus spp.*, *Acer spp.*, *Crataegus monogyna*, *Prunus spp.*, and other broadleaf species) persisted and grew toward the canopy layer (Chowdhury et al., 2025). As a result of inter- and intraspecific competition, the ability of closed habitats to support *P. sylvestris* regeneration may shifted in favour of drought-tolerant taxa following the die-off event. This was also reflected in the temporal dynamics of

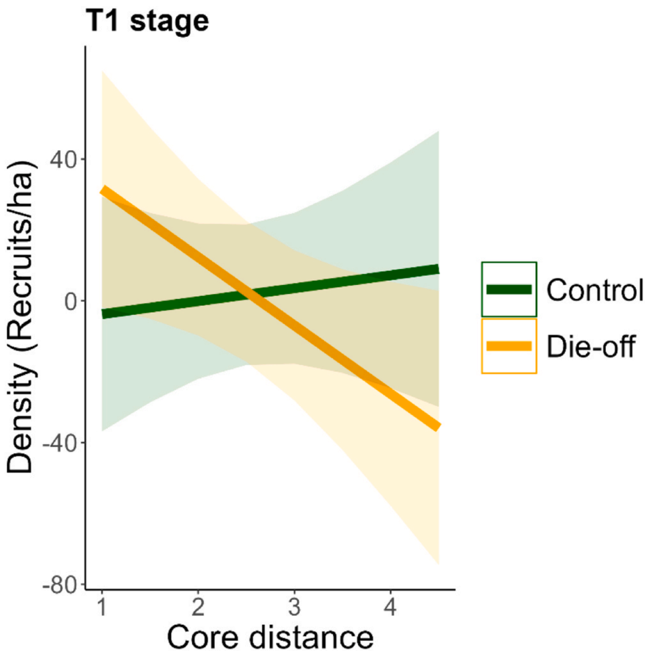

Fig. 4. Interaction effects of forest condition (die-off vs. control) and core distance in the climatic niche (see methods) on density (recruits/ha) of *P. sylvestris* at T1 development stage (seedlings), based on data pooled across years. The envelopes around effect lines denote 95 % confidence intervals. The figure reflects model predictions. Model summary and statistical significance of the interaction effects are provided in Table 1.

regeneration decline under closed canopies (Fig. 5B), reaching levels comparable to defoliated habitats when data were pooled without considering forest condition (Table 2).

However, there are methodological limitations in our study that should be considered when interpreting the results obtained for the estimation of recruits' density. Particularly, we applied a proxy-based approach to estimate recruit density by using canopy cover and tree basal area. While these proxies provide a reasonable approximation, we acknowledge that it cannot fully capture the fine-scale variability in microsite conditions experienced by recruits, although the inclusion of random variables improved the reliability of LMMs. Also, we used visual observations to estimate tree defoliation level and canopy cover in the field, which is subjected to some degree of errors in spite of cross validation between surveyors based on references from photographic records.

4.2. Interaction between climatic niche and canopy cover

Apart from the characteristics of canopy cover, the population's position in the species climatic niche determined recruitment patterns, particularly in die-off plots, where the density of seedlings declined with increasing core distance (Fig. 4). This is consistent with previous studies showing lower performance in terms of species abundance associated to drought events in populations living far from the climatic niche optimum (Margalef-Marrase et al., 2022). Our study expands this pattern to the recruitment capacities of tree seedlings in drought-affected plots.

Sapling densities also declined with increasing distance from the climatic niche core, but the magnitude of this response differed between developmental stages and canopy conditions (Fig. 6A, C; Table 1). Young saplings were consistently climate-sensitive across increasing core distance, showing strong declines in both closed and open habitats, which indicates that canopy cover did not improve their persistence under less suitable climatic conditions. In contrast, old saplings experienced this strong decline only in open habitats, while this effect was weaker beneath closed canopies, suggesting that canopy cover partially buffered them against climatic stress (Margalef-Marrase et al., 2025; Perez-Navarro et al., 2024). In climatically optimal sites, such buffering is expected to be less critical, as recruits generally experience favourable temperatures and lower water stress, allowing both young and old saplings to establish across closed and open habitats. However, toward harsher conditions near the niche edge, canopy cover would provide a degree of protection that enabled some persistence of old saplings. The deeper rooting of these saplings likely enhanced their persistence during drought stress, allowing them to take more benefit from canopy-moderated microclimates than younger saplings. Overall, this canopy-driven facilitation may delay local extinction for old saplings, creating extinction lags in regeneration trajectories (Alexander et al., 2018).

Nevertheless, defoliated habitats consistently failed to sustain regeneration across the species' climatic niche gradient. Over time, defoliation-induced regeneration failure could drive long-term ecosystem shifts (Bowd et al., 2023) across the climatic gradients in which *P. sylvestris* lives, gradually transforming forested areas into locally open woodlands or shrublands (Batllori et al., 2020; Lloret and Batllori, 2021).

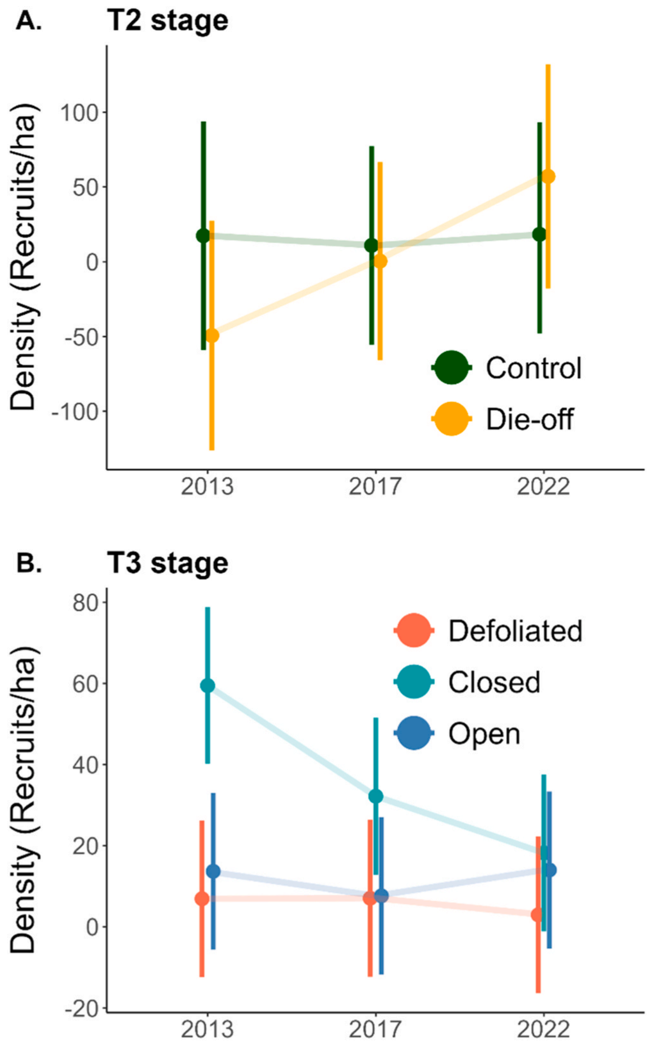

Fig. 5. Density (recruits/ha) of *P. sylvestris* at (A) T2 stage (young saplings) modelled forest condition (die-off vs. control) for the three survey years (2013, 2017, 2022), and at (B) T3 stage (old saplings) modelled by canopy cover type (closed, defoliated, and open) for the three survey years. The figure reflects model predictions. The dots denote point estimates, while error bars represent 95 % confidence intervals. Model summary and statistical significance of the related interaction effects are provided in Table 1.

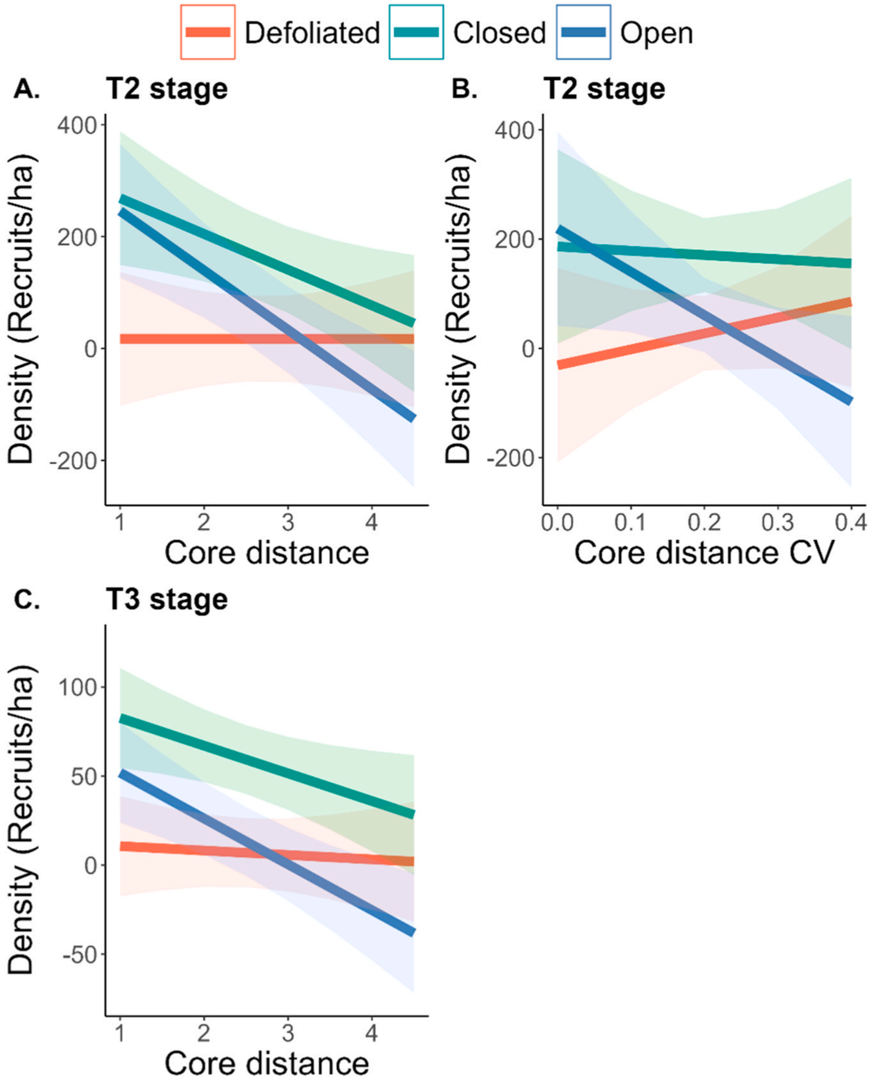

Fig. 6. Interaction effects between canopy cover type (closed, defoliated, open) with (A) core distance and (B) core distance variability (coefficient of variation, CV) on T2 (young saplings) density (recruits/ha) of *P. sylvestris* recruits, and between (C) canopy habitat and core distance on T3 (old saplings) density (recruits/ha). The figure reflects model prediction, based on data pooled across years. The envelopes around effect lines denote 95 % confidence intervals. Model summary and statistical significance of the interaction effects are provided in Table 1.

4.3. Interaction between climatic niche variability and canopy cover

The negative consequences of interannual climate fluctuations (i.e., variability relative to the core distance) on *P. sylvestris* recruitment were more evident in open habitats, where increased irradiance combined with limited water availability may have contributed to young sapling decline during very dry or warm years. Such fluctuations were likely associated with unusually dry or warm years before and after the drought-driven die-off event (Figure S1A, B). In contrast, closed canopies likely buffered young saplings during these years of high climatic fluctuation, helping to maintain their abundance (i.e., a non-significant decline compared to defoliated habitat; Fig. 6B; Table 1). Thus, temporal maintenance in climatic conditions appears relevant for recruitment success alongside historical climatic suitability.

Finally, the increase in young sapling density in die-off plots only became evident almost a decade after the drought (Fig. 5A) and may reflect a recent shift from harsher to milder local climate conditions - particularly in terms of precipitation - in some sites (Figure S1). This is supported by the observed shift in the climatic niche position of certain *P. sylvestris* populations, which have transitioned from previously marginal locations into more climatically suitable conditions (Fig. 2B, Figure S4). In addition, the accumulation of deadwood in die-off plots may enhanced microsite conditions for young saplings, gradually assisting the transition of seedlings into the young sapling stage (Thom et al., 2023). Thus, regeneration success appears to be shaped by both site-level disturbance legacies and broader meso-climatic trends (Batllori et al., 2020; Jackson et al., 2009; Perez-Navarro et al., 2024, 2021). Nonetheless, more fine-scale information is needed to explain this phenomenon more precisely.

5. Conclusion and management implications

Our findings show that *P. sylvestris* regeneration success following drought-induced die-off is shaped by canopy structure and the position of populations in the species' climate niche, with differences across recruitment development stages. Die-off reduced both young and old saplings in closed habitats, likely influenced by species turnover toward more drought-tolerant accompanying taxa. Regeneration consistently failed in defoliated habitats, regardless of climatic suitability or recruits' development stages. Open habitats in die-off plots promoted seedling emergence and progression to later sapling stages. In this habitat, higher sapling abundance appeared in sites near to species' climatic optimum.

However, in climatically marginal sites, open conditions became limiting, and regeneration was restricted to only old saplings persisting under closed canopy refugia.

These results highlight the importance of maintaining canopy structural heterogeneity to support regeneration across varying climate contexts. Management strategies such as continuous cover silviculture are well-suited to promote this structural diversity (Gonçalves, 2023), particularly by conserving closed canopy refugia in marginal climatic sites to buffer extreme climatic stress, while maintaining open conditions in optimal sites to promote seedling establishment and their progression to saplings. Deadwood retention likely acted as a key structural component, along with favourable climatic fluctuations, that gradually enhanced microsite conditions for young sapling survival. Accordingly, we found higher seedling densities in die-off plots near the species' climatic optimum and noted an increase in young sapling densities nearly a decade after the drought and subsequent die-off event. Thus, to support natural regeneration and the long-term resilience of *P. sylvestris* stands under climate stress, we recommend adaptive forest management following drought-induced die-off events. This should incorporate canopy structure management and deadwood retention, while explicitly considering the species' climate niche.

CRediT authorship contribution statement

Faqrul Islam Chowdhury: Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Josep Maria Espelta:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Teresa Sánchez-Mejía:** Writing – review & editing, Validation. **Jordi Margalef Marrase:** Writing – review & editing, Investigation, Data curation. **Luciana Jaime:** Writing – review & editing, Investigation. **Francisco Lloret:** Writing – review & editing, Supervision, Investigation, Conceptualization.

Declaration of Competing Interest

The 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.2025.123438.

Data availability

Data will be made available on request.

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